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Taxonomic assessment of *Sorbus* subgenus *Aria* in the Malé Karpaty Mountains

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Abstract: In this paper we present a taxonomic assessment of *Sorbus* subgen. *Aria* in the Malé Karpaty Mts (western Slovakia and north-eastern Austria). Detailed field observations, morphological comparison, herbarium revisions, multivariate morphometric analyses, flow cytometry and molecular (nuclear microsatellite markers) analyses were used to assess the taxonomic diversity within this group. Diploids, triploids and tetraploids were detected. Diploids are represented by a single taxon, *S. aria*, which shows considerable morphological and genetic variability. *Sorbus aria* ranges from rare to locally abundant throughout the area studied. Triploids are confined to the central and southern parts of the region and include several single, presumably apomictic individuals and rare apomictic lineages, which are not treated as separate species here due to the very limited number of individuals recorded. Tetraploids show similar distribution patterns to those of triploids: *S. danubialis* and *S. collina* occur in the southern part of the mountains, while *S. petraea*, a new species described here, inhabits the central part of the mountain range. The entire population of *S. petraea* includes approximately one hundred individuals. It occurs mainly in the surroundings of Vysoká Mt. by the village of Kuchyňa, where it forms several small populations and approximately 30 individuals grow on Čierna skala hill by the village of Plavecký Mikuláš. In addition to these recent occurrences, there are two herbarium specimens from the 1960s documenting the species on Vápená Mt. The low genetic and morphological variability and flow cytometric seed screening indicate an apomictic mode of reproduction in this species and justify its recognition at the species level. Sorbus collina is reported here in Slovakia for the first time. We have not confirmed the occurrence of *S. austriaca*, *S. buekkensis*, *S. carpatica*, *S. graeca*, *S. pannonica*, *S. thaiszii* and *S. zolyomii* in the Malé Karpaty Mts and consider the previously published records to be erroneous. Lectotypes are designated for *S. thaiszii* and *S. zolyomii.* A determination key, detailed distribution maps and photographs of representative herbarium specimens of all taxa of *S.* subgen. *Aria* occurring in the Malé Karpaty Mts are provided. A line drawing and a photograph of the newly described species are also presented.

Keywords: Austria, chorology, DAPI flow cytometry, new species, nuclear microsatellite markers, *Rosaceae*, Slovakia, *Sorbus aria* group, *Sorbus petraea*, taxonomy

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Introduction

The genus *Sorbus* L. s.l. is one of the most taxonomically challenging groups of vascular plants in Europe. Taxonomic difficulties result from two types of issues. The first problem stems from the morphological variability of the genus *Sorbus* in the broadest sense. Phylogenetic studies indicate that the traditionally recognized genus *Sorbus* s.l. is polyphyletic and should be split into several genera (Robertson et al. 1991, Potter et al. 2007, Li et al. 2012, Lo & Donoghue 2012, Sun et al. 2018). However, other authors have proposed the inclusion of *Sorbus* s.l. and some other genera in *Pyrus* L. s.l. (Christenhusz et al. 2018). Due to a lack of consensus on a new taxonomic treatment and nomenclature (Mezhensky et al. 2012, Sennikov & Kurtto 2017, Christenhusz et al. 2018, Sennikov 2018) and for pragmatic reasons, we adopt here a conservative approach, i.e. the traditional classification of the genus into five subgenera: *Sorbus* subgen. *Aria* Pers. [including *S. aria* (L.) Crantz, *S. umbellata* (Desf.) Fritsch and polyploid apomictic taxa], *S.* subgen. *Chamaemespilus* (Medik.) K. Koch [*S. chamaemespilus* (L.) Cratnz], *S.* subgen. *Cormus* (Spach) Duch. (*S. domestica* L.), *S.* subgen. *Sorbus* (*S. aucuparia* L.) and *S.* subgen. *Torminaria* (DC.) C. Koch [*S. torminalis* (L.) Crantz] (Kutzelnigg 1995, Rich et al. 2010). This approach is in line with some other recent studies (e.g. Levin et al. 2018, Lepší et al. 2019, Qiu et al. 2019, Meyer et al. 2020, Németh et al. 2020).

The second type of taxonomic problem within the genus stems from its huge taxonomic diversity, which is generated by frequent interspecific hybridization, genome duplication and subsequent stabilization of the crosses by apomixis. *Sorbus aucuparia*, *S. chamaemespilus* and *S. torminalis* hybridize relatively frequently with *S*. subgen. *Aria* and produce polyploid apomictic complexes. Their members are morphologically mutually close because they may originate polytopically from the same or related parents. However, the genetic and morphological uniqueness of these lineages, their stability maintained by apomixes and their characteristic distribution allow them to be viewed as separate apomictic species (Meyer et al. 2005, Cornier 2008, Rich et al. 2010, Grundt & Salvesen 2011, Németh 2012, Vít et al. 2012).

From taxonomic and evolutionary perspectives, the most challenging group of the genus *Sorbus* in Europe is *S.* subgen. *Aria*. Its considerable taxonomic diversity and complexity have been generated by extensive hybridization within the subgenus due to the weak reproductive barriers between its members (Feulner et al. 2013, Lepší et al. 2019).

It is supposed that most species distinguished within the *Sorbus* subgen. *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 1943, 1955, Kutzelnigg 1995). Polyploids originating from hybridization or polyploidization of these two basic species may have relatively large distributions, which applies to the following taxa: *S. baldaccii* (C. K. Schneid.) Zinserl. (the Balkan Peninsula), *S. collina* M. Lepší, P. Lepší et N. Mey. (central Europe), *S. danubialis* (Jáv.) Prodan (central Europe), *S. hibernica* E. F. Warb. (Ireland), *S. obtusifolia* (DC.) Prain (southern Norway and Sweden), *S. porrigentiformis* E. F. Warb. (Wales, England), *S. rupicola* (Syme) Hedl. (Scandinavia, British Isles). Another 47 currently distinguished species (Kurtto et al. 2018, Raimondo et al. 2019, Meyer et al. 2020) within this subgenus in Europe are local endemics and are generally considered to be the results of hybridization between the widely distributed polyploids and *S. aria* s. str. (Rich et al. 2010, Lepší et

al. 2015). In central Europe, three widely distributed taxa from the *S.* subgen. *Aria* occur: sexual and diploid *S. aria* and two apomictic tetraploids, *S. danubialis* and *S. collina*. Triploid and tetraploid taxa or morphotypes intermediate between *S. aria* and the two tetraploids are reported, mostly from contact zones of these three species (Feulner et al. 2013, Lepší et al. 2015, Somlyay et al. 2016).

From Slovakia, where most of the area studied is located, seven taxa from the subgenus are listed in Atlas Florae Europaeae (Kurtto et al. 2018). They are *Sorbus aria*, *S. danubialis*, *S. graeca* (Spach) Schauer s.l., *S. javorkana* Somlyay, Sennikov et Vojtkó, *S. subdanubialis* (Soó) Kárpáti, *S. thaiszii* (Soó) Kárpáti and *S. zolyomii* (Soó) Kárpáti. From Austria, only five species are reported: *S. aria*, *S. collina*, *S. cucullifera* M. Lepší et P. Lepší, *S. danubialis* and *S. thayensis* M. Lepší et P. Lepší. However, the real species diversity, especially in Slovakia, is probably higher and remains unknown due to a lack of taxonomic research.

The Malé Karpaty Mts are well known for the high diversity of endemic species from the hybridogenous *Sorbus* subgen. *Tormaria* Májovský et Bernátová. Today, five species are accepted for this mountain range (Kurtto et al. 2018). In contrast, the *S.* subgen. *Aria* is represented in this contemporary compendium by four taxa, none of which is supposed to be endemic to the region: *S. aria*, *S. danubialis*, *S. graeca* and *S. zolyomii* (Kurtto et al. 2018), and another three species have been reported by *Sorbus* specialists from the area in the past: *S. buekkensis*, *S. pannonica* and *S. thaiszii* (Kárpáti 1960, Kovanda 1961, Dostál 1989, Májovský 1992, Jakubowsky 1996).

The oldest records of the occurrence of *Sorbus* subgen. *Aria* in the Malé Karpaty Mts were published under the names "*Crataegus aria*" and "*Pyrus aria*" (both nomenclatural synonyms of *S. aria*) in the second half of the 18th century (Lumnitzer 1791) and first half of the 19th century (Endlicher 1830), and both of them were located on the Devínska Kobyla hill. Another record of the *S.* subgen. *Aria* from the region relates to *S. danubialis*, which is reported from Devín (Slovakia) in the protologue in Jávorka (1915) and then steadily reported from this region in most floras and important publications dealing with *Sorbus* (Jávorka 1924, Domin & Podpěra 1928, Klika 1937, Dostál 1948). During the 20th century, three other taxa originally described from Hungary were added to the list of plants of the area studied. At first, Soó (1937) noted the occurrence of *S. zolyomii* from Vápenná Mt. near Sološnica, then Kárpáti (1960) provides three localities (Vápenná Mt., Devínska Kobyla hill, Bratislava) of *S. pannonica* and Kovanda (1961) gives an account of *S. buekkensis* and *S. zolyomii* in the Čachtice hills. Further species reported from the area studied relatively recently are *S. graeca* and *S. thaiszii*. The first was reported from Devínska Kobyla hill and generally from the Malé Karpaty Mts (Májovský 1992) and Hainburger Berge hills (Jakubowsky 1996) and the second from Hainburger Berge hills (Jakubowsky 1996).

The application of modern methods has recently shown that the determinations of *Sorbus* species based only on morphology can be burdened with errors (Vít et al. 2012, Meyer et al. 2014, Lepší et al. 2015). Therefore, we performed a detailed taxonomic revision of the list of all species of the *Sorbus* subgen. *Aria* reported from the Malé Karpaty Mts using traditional and contemporary biosystematic methods. This paper presents the results of this assessment and provides basic information about the morphology, distribution and taxonomy of all the species recorded. As a result of this study a distinct population located in the central part of the Malé Karpaty Mts is described here as a new species, *Sorbus petraea*.

Material and methods

Delimitation of the area studied

The area studied covers the whole range of the Malé Karpaty Mts, which are situated in two central-European countries, western Slovakia and north-eastern Austria. The mountain range is low (from 132 to 768 m a.s.l.), approximately 100 km long and stretches from Slovakian Nové Mesto nad Váhom in the north to Austrian Hainburg an der Donau in the south. In Slovakia, the region is bordered by the Záhorská lowland and Slovak-Moravian Carpathians (Myjavská pahorkatina hilly area, Považské Podolie valley) in the west and north and by the Danubian lowland in the east (Mazúr & Lukniš 2002). In Austria, the mountain range is limited to several hills called the Hainburger Berge hills and this area is separated from the main Slovakian part of the mountains by the Danube river valley. In terms of phytogeography, the northern and larger parts of the area studied belong to the West Carpathian floristic region and the southern part to the Pannonian region (Futák 1984, Fischer et al. 2008). The mean annual precipitation ranges between 550 and 800 mm (Faško & Šťastný 2002) and mean annual air temperature varies from 6 °C on the summits of the mountain range to 9 °C in the lowlands (Šťastný et al. 2002). The basic geochemical types of rock are: (i) granitoids, (ii) metapsammites, metapelites, predominantly acid metavolcanites and metavolcanoclastic rocks and intermediary to basic metavolcanites and metavolcanoclastic rocks with layers of poorly metamorphosed limestones, dolomites and magnesites, and (iii) limestones and dolomites (Marsina & Lexa 2002).

Plant material and field work

Plant material was sampled between 2014 and 2020 following the recommendations of Meyer et al. (2005) and Rich et al. (2010) and papers published by Lepší et al. (2008, 2009). Mature and well-developed individuals were used for the study of phenotypic, cytological and genetic variation. For the morphological description, flowering and fructiferous parts were collected in mid-May and August or September, respectively, and stored in the herbarium and/or in 70% ethanol. For multivariate analyses, only well-developed, mature and intact leaves from the centre of short sterile shoots were collected, flattened and dried. Unless otherwise specified, the leaves mentioned in the text refer to those of sterile short shoots. Prior to flow cytometry analysis, fresh leaves were kept in plastic bags and stored at 4 °C for a few days. For DNA extraction, samples of leaf tissue were collected and quickly desiccated in silica gel. In addition to samples from the area studied *Sorbus* taxa were sampled in adjacent regions and countries for comparison. All analysed taxa and locality details are listed in Supplementary Table S1. Altitudes and coordinates (WGS 84) were determined using a Garmin GPSMAP 60CSx instrument.

For the taxonomic revision of the relevant *Sorbus* material the following public herbarium collections were examined (Thiers 2021, for BBZ see Vozárová & Sutorý 2001): BBZ, BP, BRA, BRNL, BRNM, BRNU, CB, CHEB, HOMP, LI, LIT, OL, PL, PR, PRA, PRC, ROZ, SAV, SLO, SOB, SOKO, SZB, SZU, W and WU. Herbarium specimens in the private collection of J. Velebil stored in Silva Tarouca Research Institute for Landscape and Horticulture in Průhonice are designated as “herb. J. Velebil”. The localities were first arranged by country, then according to the central-European grid mapping scheme

(Ehrendorfer & Hamann 1965) and subsequently by locality. In special cases for explanation of special terms or local geographic names, information in non-English written herbarium labels was translated into English and put into square brackets. Coordinates missing on herbarium sheets were added using online maps (http://www.mapy.cz) and enclosed in square brackets. Acronyms of public herbaria follow accession numbers of specimens if known. Names of the most frequent collectors are abbreviated: JN = J. Nosková, JV = J. Velebil, ML = M. Lepší, PL = P. Lepší. The abbreviation FCM means that the plant was analysed using flow cytometry and the abbreviation ID follows the collection numbers of specimens. Finally, original determination and revision (if they exist) are attached in square brackets at the end of the locality record. For the list of herbarium specimens studied see Supplementary Data S1.

Estimation of somatic DNA ploidy level

The DNA ploidy level of 126 adult trees was estimated using DAPI (4',6-diamidino-2-phenylindole) flow cytometry. *Bellis perennis* L. (2C = 3.38 pg; Schönswetter et al. 2007) or *Carex acutiformis* Ehrh. (2C = 0.86 pg; Lipnerová et al. 2013) were used as an internal standard. Leaf tissue (0.5 cm^2) of the analysed sample and an appropriate volume of the internal standard were chopped together in a Petri dish containing 0.5 ml Otto I buffer (0.1 M citric acid monohydrate, 0.5% Tween 20; Otto 1990). The nuclear suspension was then filtered through a 42 μm nylon mesh. After 10 min of incubation at room temperature, a staining solution consisting of 1 ml of Otto II buffer (0.4 M $Na_2HPO_4 \cdot 12\ H_2O$; Otto 1990) supplemented with DAPI (final concentration 4 μg/ml; Sigma) and 2-mercaptoethanol (2 μl/ml) was added. The relative fluorescence intensity for 3,000 particles was measured on a CyFlow ML (Partec GmbH, Germany, now Sysmex) equipped with a UV LED (365 nm). Fluorescence histograms were further analysed using FloMax 2.0 software (Partec GmbH, Germany, now Sysmex). Ploidy levels were deduced from the sample/standard ratios based on previous karyological studies on the genus *Sorbus* (Lepší et al. 2008, 2015).

Flow cytometric seed screen

The mode of reproduction of *Sorbus petraea* was determined using the flow cytometric seed screen methodology (Matzk et al. 2000). In total, 11 seeds from two mother trees were successfully analysed. Lateral parts of the seeds were used for the analysis. The rest of the procedure generally copied that used for the leaf analysis. Modes of reproduction were inferred based on DNA ploidy levels of embryos and endosperms following Talent & Dickinson (2007).

Molecular analysis, nuclear microsatellite markers (SSR)

Genomic DNA of 105 individuals was extracted from silica-dried leaves following the modified CTAB protocol (Doyle & Doyle 1987, Pfosser et al. 2005). Seven microsatellite primer pairs developed for the genera *Sorbus* (Mss5, Ms6g, Mss13, SA03, SA08 and SA191; Oddou-Muratorio et al. 2001, Nelson-Jones et al. 2002, González-González et al. 2010) and *Malus* (CH02D11; Gianfranceschi et al. 1998) were used for the genotyping of adult trees. Forward primers were fluorescently labelled with 6-FAM, NED or HEX

fluorescent dyes. Two multiplex PCR amplifications using a QIAGEN multiplex PCR kit were performed for each sample. The reaction of the total volume of 12 µl consisted of 6 µl of Qiagen M.mix, 1 µl of DNA (10 ng/µl), ddH_2O and 0.1 µl of each primer (Ms6g, Mss13 and SA03) in multiplex I or 0.1 µl (Mss5, SA08, SA191) and 0.07 µl (CH02D11) in multiplex II. Thermocycling conditions were 95 °C for 15 min; 35 cycles of 94 °C for 30 s, 55 °C for 90 s and 72 °C for 60 s; and a final extension of 60 °C for 30 min. Amplification products were separated using a 3130xl Genetic Analyzer (Applied Biosystems) using a GeneScan ROX 500 size standard (Applied Biosystems). Fragment sizes were scored manually by GeneMarker 1.8.0 (SoftGenetics).

Based on the different ploidy levels of the samples analysed, the microsatellite pattern was scored as an "allele phenotype" (Becher et al. 2000), followed by conversion of the data set to a binary matrix. For differentiation of individual groups (taxa), we plotted genetic distances among individuals using principal coordinate analysis (PCoA) based on Jaccard distance calculated in PAST (v. 2.17; Hammer et al. 2001). Intraspecific variation was measured using Arlequin ver. 3.5 computer program (Excoffier & Lischer 2010), which computes the average gene diversity of all loci (AGD; Nei 1987).

Multivariate morphometric analyses

Multivariate morphometric analyses were used to reveal species-specific characteristics of leaves of the newly discovered species and how it differs from *Sorbus danubialis* and *S. collina*, the two tetraploids cooccurring in the area studied. Ten individuals per species were sampled of *S. danubialis* in southern Moravia (Podyjí National Park), *S. collina* from central Bohemia (Střední Povltaví region, Český Kras karst) and *S. petraea* from the surroundings of Vysoká Mt. A set of 13 characters was chosen based on published determination keys and floras (e.g. Kutzelnigg 1995, Meyer et al. 2005, Rich et al. 2010), including those used in related studies (Lepší et al. 2008, 2009, 2015). The characteristics were: 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, INC – depth of the incision between the 2nd and the 3rd lateral veins from the laminar base, LL – length of lamina, LL/LW – lamina length/width ratio, LW– width of lamina, NT3L – number of teeth between the 2nd and 3rd lateral veins, NV – number of lateral laminar veins, PET – length of petiole, WP – distance along the main vein from the laminar base to its widest part, WP/LL – ratio of the distance along the main vein from the laminar base to its widest part/length of lamina. Dried leaves were scanned at 300 dpi using Epson scan 1.11E software and then measured using tpsDig software (Rohlf 2006). One measurement of each character per individual was recorded and used as the value for the individual in all morphometric analyses.

Nonparametric Pearson correlation coefficients were calculated for pairs of characters of each species and for the whole dataset to reveal relationships among characters. Principal component analyses (PCAs) were performed to provide an insight into the overall pattern of morphological variation and reveal the potential separation of the species analysed. Prior to PCA, the data were log-transformed and standardized to have a zero mean and unit standard deviation. Linear discrimination analyses (LDAs), which maximize differences between a priori defined groups (species characterized by SSR patterns), were used to test the discriminating power of morphometric characters, following the

methodology described by Lepš & Šmilauer (2003) using forward selection of characters with nonparametric 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 (minimum, maximum, quartiles) of quantitative characters of all individuals were calculated and used in the description of the species.

Results and discussion

The results of flow cytometry, molecular and morphometric analyses are congruent with each other and support the taxonomic solutions presented below.

Ploidy level and modes of reproduction

Three ploidy levels were recorded within *Sorbus* subgen. *Aria* in the Malé Karpaty Mts: diploid (*S. aria*), tetraploid (*S. collina*, *S. danubialis*, *S. petraea* and single biotypes) and triploid (single biotypes and rare lineages). No intraspecific variation was detected. The recorded sample/standard ratio for each sample, coefficient of variation (CV) of the sample and standard and their averages for each ploidy level and taxon are listed in Supplementary Table S2, S3 and S4. All analysed seeds of *S. petraea* were of apomictic origin, which included fertilization of polar nuclei, i.e. pseudogamy.

Molecular analyses: nuclear microsatellite markers

Based on the microsatellite pattern, we were able to clearly distinguish four groups in the Malé Karpaty Mts (Fig. 1). Three of these groups correspond to the microsatellite patterns of *Sorbus aria*, *S. collina* and *S. danubialis* sampled throughout central Europe. The fourth well-separated group belongs to *S. petraea* described as a new species below. The most genetically diverse species in the Malé Karpaty Mts is the amphimictic *S. aria* in which each of the 8 samples analysed had a unique microsatellite pattern and the average gene diversity over all loci (AGD) was 0.1918±0.1108. The variability of the three apomictic taxa is an order of magnitude lower. In *S. petraea*, we detected four genotypes (22 individuals sampled) and the AGD was 0.0051±0.0056. In *S. danubialis*, we detected four genotypes in four samples (AGD not specified due to a low number of samples from the area studied) and in *S. collina* 11 genotypes in 15 samples and AGD 0.0537±0.0320. A similar level of molecular variability is recorded in *S. aria* and apomictic species in related studies (Lepší et al. 2009, Vít et al. 2012, Feulner et al. 2013) and is in accordance with our unpublished data from adjacent areas.

In addition, we detected triploid and tetraploid individuals that differed significantly from all of the above-mentioned species in terms of their molecular patterns. Three tetraploid individuals showed three distinct allele phenotypes, and 20 triploid individuals had 12 distinct allele phenotypes. Within triploids, we detected four small lineages with the same but mutually distinct allele phenotype. One of these lineages occurred at two

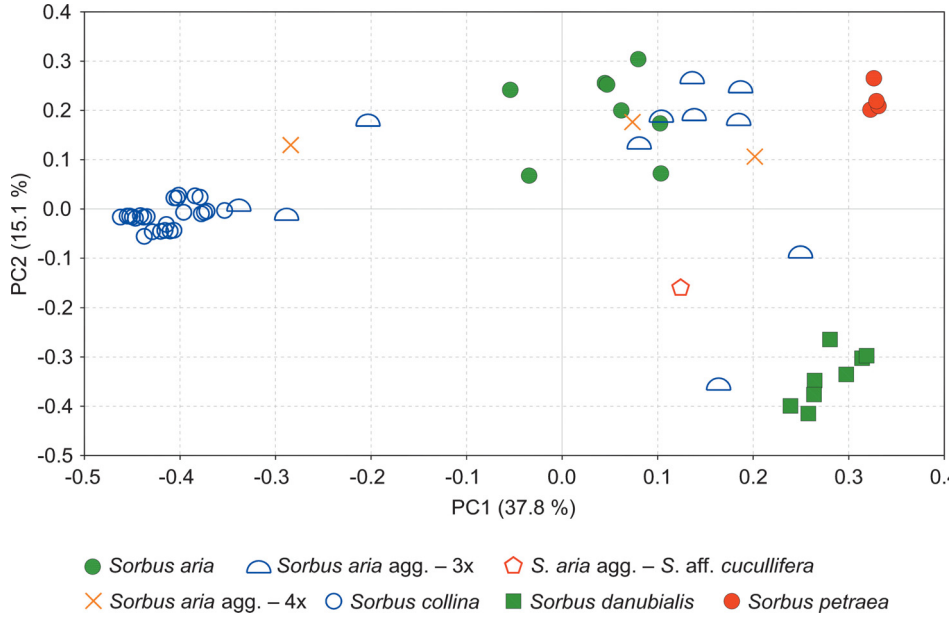

Fig. 1. Principal coordinate analysis of *Sorbus* microsatellite data based on Jaccard distances of 105 *Sorbus* individuals from Malé Karpaty Mts and adjacent regions. The first and second ordination axes explain 37.8% and 15.1% of the overall variation, respectively.

localities and included six individuals and the remaining three lineages included two individuals each from three different localities. The six-membered lineage was shown to be phenotypically uniform and similar in leaf morphology to *Sorbus cucullifera*; therefore, their relationship to this species was tested. The comparison of the microsatellite patterns of these two similar *Sorbus* populations showed that they differed significantly and formed two separate groups (data not shown).

The microsatellite pattern of *Sorbus thaizsii* and *S. zolyomii*, the two species originally described from eastern Slovakia and northern Hungary and reported in the literature from the Malé Karpaty Mts differ significantly from each other and from all *Sorbus* sampled in the area studied (data not shown).

Multivariate morphometric analyses

No highly correlated characters (r >|0.95|) were found and all characters were used in the multivariate analyses. PCA showed clear morphological differentiation between the three taxa studied (Fig. 2). The first axis separates *Sorbus petraea* and the two remaining tetraploids. The characteristics contributing most to the first principal component (explaining 30.4% of the overall variation) were: lamina length/width ratio (LL/LW), angle of the tooth in which the 3rd lateral vein terminates (A3L), angle of the laminar base (AB), depth of the incision between the 2nd and the 3rd lateral vein from the laminar base (INC) and length of petiole (PET). The second axis separates *S. collina* and *S. danubialis*. The most tightly correlated characters with the second axis (explaining 23.0% of the overall variation) were length of the lamina (LL), width of the lamina (LW), angle of the

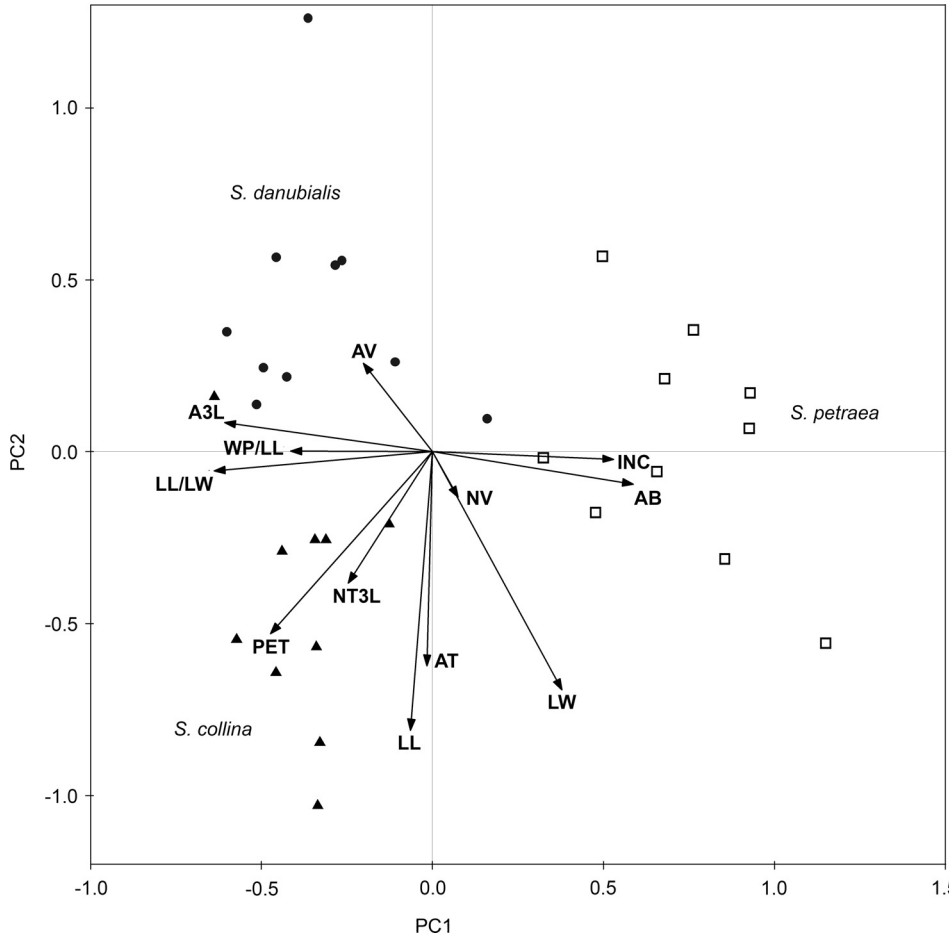

Fig. 2. Principal component analysis based on twelve morphological characters of leaves of the three species of *Sorbus* subgen. *Aria*. The first and second ordination axes are displayed. These explain 30.4% and 23.0% of the overall variation, respectively. For abbreviations of characters, see the Material and methods.

lamina top (AT) and length of the petiole (PET). A subsequent LDA also revealed that these three species are morphologically distinct as there is no overlap in the canonical scores (Fig. 3). The forward selection procedure identified 5 characters with a significant conditional effect: angle of the tooth in which the 3rd lateral vein terminates (A3L), angle between the third lateral vein from the laminar base and the midrib (AV), angle of laminar base (AB), angle of the lamina top (AT) and length of petiole (PET); all characters except for number of teeth between the 2nd and 3rd lateral vein (NT3L), angle between the third lateral vein from the laminar base and the midrib (AV) and number of lateral laminar veins (NV) had significant marginal effects. The first axis (explaining 44.0% of the overall variation) similar to the PCA separates *S. petraea*, whereas the second axis (explaining 42.7% of the overall variation) separates *S. danubialis*. The most tightly correlated characters with the first axis were length of petiole (PET), angle of the tooth in which the 3rd lateral vein terminates (A3L), angle of laminar base (AB) and the most tightly correlated

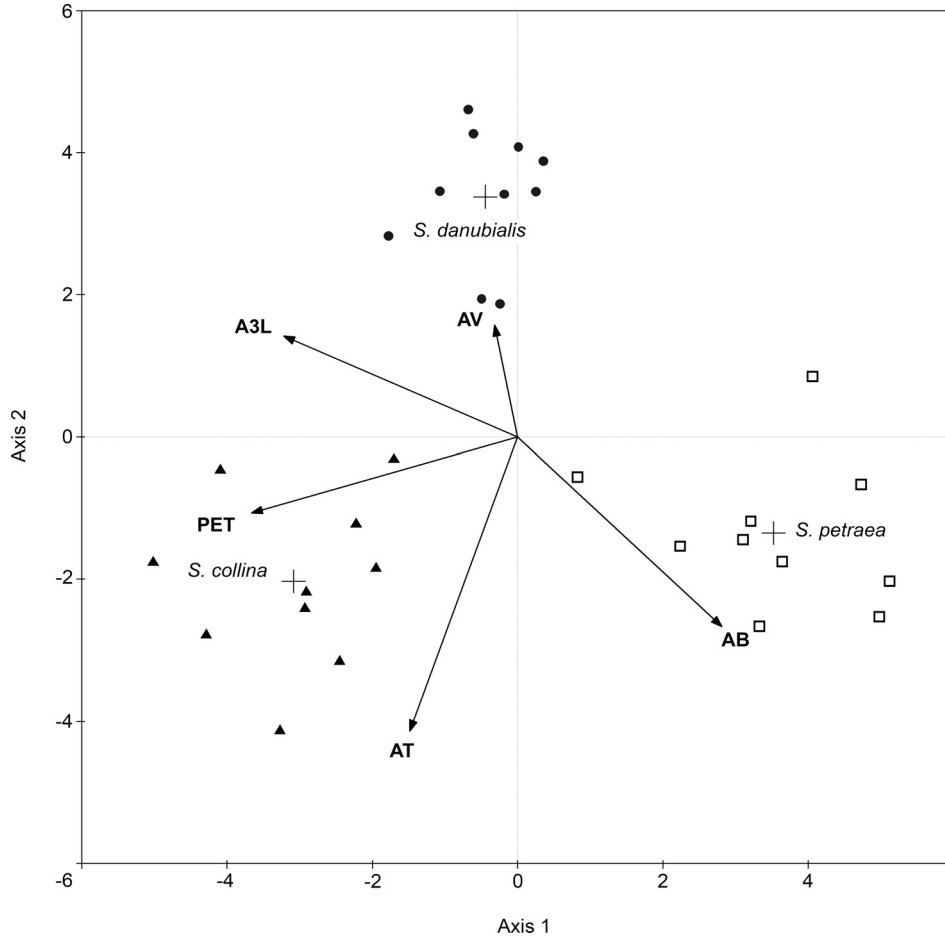

Fig. 3. Linear discriminant analysis based on 5 morphological characters of leaves of the three species of *Sorbus* subgen. *Aria*. The characters were selected in a forward selection procedure and only those with significant discriminating power for separating the three species were used. The first and second canonical axes are displayed, which explain 44.0% and 42.7% of the variation, respectively. For abbreviations of characters, see the Material and methods.

characters with the second axis were angle of the lamina top (AT), angle of laminar base (AB) and angle between the third lateral vein from the laminar base and the midrib (AV). The classificatory discriminant analysis resulted in incorrect classification in only one out of a total of 30 cases, with one individual of *S. petraea* misidentified as *S. danubialis*.

Taxonomic treatment

Based on extensive field observations, a detailed herbarium investigation and the results of all of the biosystematic methods presented above, we delimited four taxa within the *Sorbus* subgen. *Aria* in the Malé Karpaty Mts (Table 1). Detailed literature screening revealed seven species of the *S.* subgen. *Aria* reported from the Malé Karpaty Mts. These species are *S. aria*, *S. buekkensis*, *S. danubialis*, *S. graeca*, *S. pannonica*, *S. thaiszii* and

S. zolyomii. Only two of these taxa, *S. aria* and *S. danubialis*, were proven to occur in the region. Two species were newly discovered; *S. collina*, new to the flora of Slovakia, and *S. petraea*, a species newly described here. Records of the other taxa were found to be erroneous or doubtful and are discussed and summarized below. Finally, we found that records of the occurrence of *S. austriaca* and *S. carpatica* both classified to *S.* subgen. *Soraria* Májovský et Bernátová relate in reality to *S. aria*.

Table 1. Overview of the *Sorbus* taxa studied, species distributions and comparison of previous knowledge with new information presented in this paper. The overall distribution, and territory abbreviations, are taken from AFE (Kurtto et al. 2018), except for *S. austriaca* and *S. petraea*.

Taxon	Overall (native) distribution	Type material seen – herbarium acronym	Conclusions reached in this paper
S. aria	Europe except for By, Cm, Cr, Da, Es, Fe, Hb, Ho, Is, La, Lt, Mo, No, Rus, Su, Tu, Uk	lectotype – BM, epitype – CB	confirmed for the Malé Karpaty Mts
S. austriaca	with certainty only Au	lectotype – PRC	does not occur in the Malé Karpaty Mts
S. buekkensis	Hu?, Sk?	type not designated	does not occur in the Malé Karpaty Mts
S. carpatica	?	type not designated	does not occur in the Malé Karpaty Mts
S. collina	Au, Cs, Ge, Hu	holotype – CB	a new species for the Malé Karpaty Mts, as well as for Slovakia
S. danubialis	Au, Cs, Ge, Hu, Sk	lectotype – BP	confirmed for the Malé Karpaty Mts
S. graeca	Al, BH, Bu, Cg, Cr, Ct, Gr, Hu, It, Ko, Mk, Po, Rm, Se, Sk, Sl	lectotype – P	does not occur in the Malé Karpaty Mts
S. pannonica	Hu	lectotype – BP	does not occur in the Malé Karpaty Mts
S. petraea	Sk	holotype – CB (Fig. 6)	taxonomic novelty
S. thaiszii	Hu, Sk	lectotype – BP (Supplementary Fig. S10), epitype – CB (Supplementary Fig. S11)	does not occur in the Malé Karpaty Mts
S. zolyomii	Hu, Sk	lectotype – BP (Supplementary Fig. S12), epitype – CB (Supplementary Fig. S13)	does not occur in the Malé Karpaty Mts

Diploids

Sorbus aria (L.) Crantz, Stirp. Austr. 2: 46. 1763.

Lectotype designated by Aldasoro et al. (2004): Hortus Cliffordianus 187, BM 000628615. Epitype designated by Lepší et al. (2015): Lower Austria, Hardegg, "pine forest I" on slopes of Dyje valley, ~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 ~7 m high, 12 IX 2011 leg. M. Lepší & P. Lepší, CB 79814.

Synonyms: Sennikov & Kurtto (2017). Description and iconography: Lepší et al. (2015), Supplementary Fig. S1.

Sorbus aria is genetically a very variable species. This variability is manifested in the morphology of the species mainly in the shape and size of the leaf lamina and character of its margin. This remarkable phenotypic diversity has led to the description of many taxa at the species or lower levels in the past. However, many of these taxa were recently classified as synonyms of *S. aria* and are considered taxonomically superfluous (see Sennikov & Kurtto 2017). The high morphological variability of this species together with poor knowledge about its mode of reproduction, genetic and morphological variability, cytology and geographical distribution of many related and similar polyploid species of the *S.* subgen. *Aria* has led to many determination mistakes. Individuals of *S. aria* have often been erroneously determined as different species of *S.* subgen. *Aria* but also of *S.* subgen. *Soraria* (for instance, as *S. austriaca*, *S. carpatica*; Lepší et al. 2015). Our revision of *S.* subgen. *Aria* in the Malé Karpaty Mts confirmed the extensive morphological and molecular variability in *S. aria* and revealed several taxonomic inconsistencies and determination mistakes that stemmed from the above outlined issues. Some individuals of *S. aria* from the Malé Karpaty Mts were mistakenly identified as *S. austriaca* (Domin & Podpěra 1928, Klika 1936, Dostál 1948, 1989, Májovský & Uhríková 1990, Májovský 1992, Marhold et al. 2007), *S. buekkensis* (Kovanda 1961), *S. graeca* (Dostál 1989, Májovský 1992), *S. pannonica* (Kárpáti 1960, Dostál 1989, Májovský 1992) or *S. zolyomii* (Soó 1937, Kovanda 1961, Kurtto et al. 2018). Two other names misused for *S. aria* are *S. carpatica* (Klika 1937, Kárpáti 1960, Dostál 1989, Májovský & Uhríková 1990, Májovský 1992, Jakubowsky 1996, Marhold et al. 2007) and *S. aria* var. *cyclophylla* (Klika 1937).

Historical records: The oldest herbarium specimen documenting the occurrence of this species in the study area dates to May 17, 1864 (leg. D. W., depon in W), and comes from Braunsberg hill near Hainburg an der Donau. There are two even older records from Devínska Kobyla hill (as *Crataegus aria*; Lumnitzer 1791 and *Pyrus aria*; Endlicher 1830). However, this species has never been documented from this intensively searched locality by any herbarium specimen and was not recorded during our field survey, and moreover, other representatives of the *Sorbus* subgen. *Aria* commonly occur there, so it is not possible to consider these old records as reliable. During the 20th century, the species was sometimes mentioned in papers dealing with *Sorbus* in this region (Klika 1937, Kárpáti 1960, Májovský 1992, Jakubowsky 1996, Marhold et al. 2007).

Distribution and population size: This south-to-central Europaean species is widely distributed in Slovakia and Austria except in extensive lowlands and their adjacent areas, which lack favourable habitats. In the Malé Karpaty Mts the distribution of this species reflects geology. It is abundant on limestone and dolomite, which occur mainly in the northern part of the mountain range, especially north of the line connecting the villages of Kuchyňa and Doľany (Biely et al. 2002, Polák 2011). In the southern parts of the area studied, this species is not recorded, such as in the Devínska Kobyla phytogeographical district, or rarely occurs on small limestone outcrops, such as in the Hainburger Berge hills. The population in the area studied is estimated at thousands of individuals.

Triploids

More than twenty triploids were recorded in the central and southern parts of this region (Fig. 4). In the central part, we recognized a morphologically homogenous and presumably apomictic lineage consisting of six individuals. The lineage is confined to the gorge between the village of Plavecký Peter and the Buková water reservoir, where it inhabits forest-steppe with *Sorbus aria* and taxa from *S.* subgen. *Tormaria*. In terms of leaf morphology, it is very similar to *S. cucullifera*, a species described from the Thaya river valley in Moravia and Lower Austria. However, the molecular analyses clearly ruled out it belonging to this taxon. In addition to this uniform population, we sampled three two-membered lineages and several single triploids on the Bačkorová hill, Dlhý vrch hill and Vysoká Mt. The triploids from Vysoká Mt. could have originated from hybridization between co-occurring *S. petraea* and *S. aria*. The remaining triploids occur where there are no tetraploid species and their origin is thus unclear. They could be a product of autopolyploidization of *S. aria* or result of long-distance dispersal of triploid seeds originating far from the current locality or a relict population from the period when tetraploid species were present at this locality. In the southern part of the mountains, triploids occur scattered in Hainburger Berge hills and in the Fialková dolina gorge. These triploids are

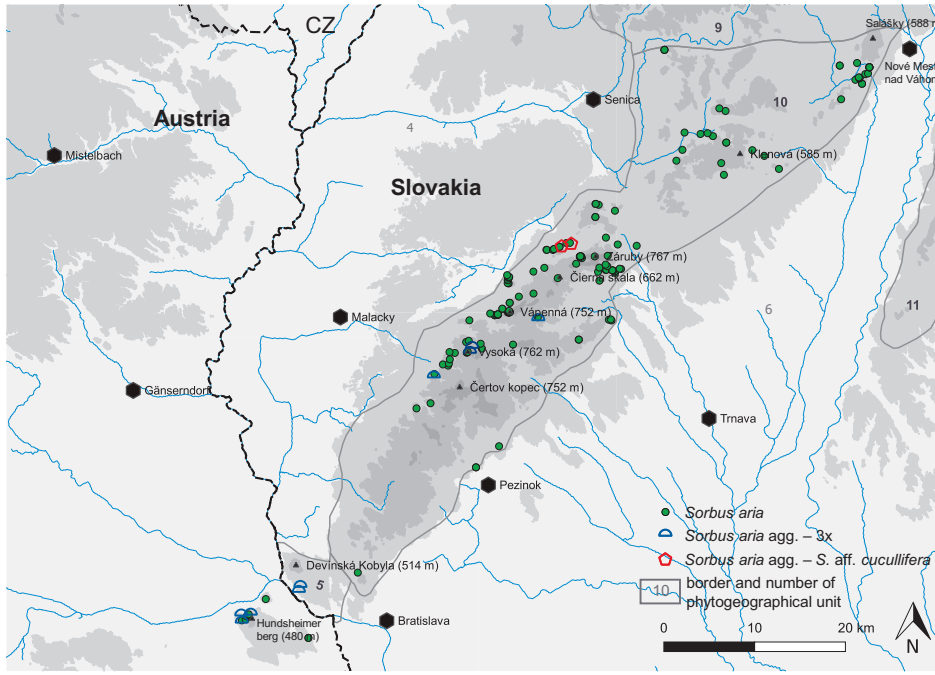

Fig. 4. Map showing the distribution of *Sorbus aria* and triploids of *Sorbus* subgen. *Aria* in the Malé Karpaty Mts based on localities documented by herbarium specimens. The names of phytogeographical units in Slovakia are: 4 – Záhorská nížina, 5 – Devínska Kobyla, 6 – Podunajská nížina, 9 – Južné Biele Karpaty, 10 – Malé Karpaty, 11 – Považský Inovec (Futák 1984). Map source: EEA (2012), OpenStreetMap (2014), Eurostat (2020), Jarvis et al. (2008).

represented by several single individuals of unique morphology and microstatellite patterns and are probably the result of interactions between *S. aria* and cooccurring tetraploids *S. collina* or *S. danubialis*. Due to the very limited number of individuals recorded, we did not treat all of the abovementioned triploids taxonomically.

Historical records: There are no records of the occurrence of triploids in the area studied supported by chromosome counts or other biosystematic methods.

Distribution and population size: The number of triploids is estimated to be in the order of several tens.

Tetraploids

Sorbus collina M. Lepší, P. Lepší et N. Mey., Preslia 87: 145. 2015.

Holotype: Central Bohemia, Nalžovické Podhájí (distr. Příbram), ~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 ~7 m high, 7 VIII 2013 leg. M. Lepší & P. Lepší, CB 83296. – Isotypes BP, BRA, LI, M, PR, PRA, PRC, W).

Description and iconography: Lepší et al. (2015), Supplementary Fig. S2.

Sorbus collina was described only recently. To date, it is reported in Bavaria, Bohemia, Austria and Hungary. There are no records of its occurrence in Slovakia, which is adjacent to its known distribution (Lepší et al. 2015, Kurtto et al. 2018). Our field research indicates that this species is probably widespread in Slovakia, as we observed it not only in the Malé Karpaty Mts and other regions in western Slovakia (e.g. Tríbeč Mts, Štiavnica Mts), but also on the Gömör-Torna Karst located in the eastern part of the country. Several different names were misused for this taxon in the past in central Europe and the same applies for records coming from the Malé Karpaty Mts. The species was reported from the area studied as *S. aria* (Májovský & Uhríková 1990, Májovský 1992, Feráková & Kociánová 1997, Marhold et al. 2007; including *S. aria* f. *cyclophylla* and *S. aria* var. *cyclophylla*, Klika 1937, Kárpáti 1960), *S. graeca* (Dostál 1989, Májovský 1992, Jakubowsky 1996, Feráková & Kociánová 1997, Kurtto et al. 2018) or *S. pannonica* (Kárpáti 1960, Dostál 1989, Májovský 1992). In terms of morphology, this species is characterized by relatively large, broadly elliptical to almost rotund leaf lamina, with obtuse, rounded or truncated apex, flat uniserrate to biserrate margins and cuneate to broadly cuneate base. Its intraspecific variation is relatively low in the area studied and the same is true for most areas of its known distribution (Lepší et al. 2015). However, considerable variability is reported in Bavaria (Feulner et al. 2017).

Although there was no significant morphological differentiation among populations of *Sorbus collina* from specific regions, slight genetic differentiation occurred among the groups of samples from the Bohemia, Hungary and Malé Karpaty Mts. Moreover, genetic variation (measured by AGD) of *S. collina* in Malé Karpaty Mts is higher than the genetic variation in Bohemia and Hungary (Bílá 2015). Unexpectedly high genetic variation for agamospermous *S. collina* is also reported in Germany (Feulner et al. 2017), which might be caused by the accumulation of mutations and/or a higher level of residual sexuality.

Historical records: The oldest record of the occurrence of this species in the Malé Karpaty Mts is documented by two herbarium specimens from 1909, collected by K. Ronniger and J. Vetter (W), and Klika (1937) published the first account of this

species. Both these records are for Devínska Kobyla hill. Since then, this species has been reported under various names from the region studied (see above).

Distribution and population size: This species is confined to a few localities in the southern part of the mountains. It occurs scattered on Devínska Kobyla hill and in the adjacent Fialková dolina gorge in Slovakia and rarely on the Braunsberg, Pfaffenberg, Hundsheimer Berg and Spitzerberg hills in Austria. Generally, the local distribution of this species is not well known. The nearest localities in Austria are reported in the valleys of Kamp and Große Krems rivers and in Hungary in Bakony and Vértes hills, which is in both cases over a hundred kilometres distant from the Malé Karpaty Mts (Lepší et al. 2015, Pachschwöll 2019). Unlike *Sorbus danubialis*, this species is absent from Moravia (Kaplan et al. 2016) and reaches the local northern limit of its distribution in the area studied. The total number of individuals recorded is in the order of several tens.

Sorbus danubialis (Jáv.) Prodan, Fl. Român. 1: 553. 1923.

Lectotype designated by Kováts (1998) as "neotype", corrected to lectotype by Somlyay & Sennikov (2016): Hungary, Buda Mts, Budapest, "in monte Sashegy", 5 V 1911 leg. S. Jávorka, BP 562679.

Synonyms: Sennikov & Kurtto (2017). Description and iconography: Lepší et al. (2015), Somlyay & Sennikov (2016), Supplementary Fig. S3.

Sorbus danubialis is a central-European species known from Bavaria, Lower Austria, the Czech Republic, Slovakia and Hungary (Kurtto et al. 2018). It is characterized by its coarsely irregular double or triple serrate to lobate leaf laminas, which are usually laterally asymmetrical, undulate at the margins and mostly rounded rhombic in outline. Its variability is manifested mainly in the shape of the leaf lamina and the character of its margin, which resulted in the description of several superfluous taxa (Soó 1937, Kovanda 1961, Németh 2010, Somlyay & Sennikov 2016). Nevertheless, these morphological characteristics are significantly dependent on the environment. Part of the observed variability can be explained by genetic variation caused by residual sexuality (Bílá 2015) or hypothetically by mutation. Despite the small number of individuals of *S. danubialis* analysed from the Malé Karpaty Mts, the samples clearly cover the whole extent of the genetic variation detected in the Czech Republic and Hungary, suggesting that the real extent of variation in the area studied could be the same or even higher.

Historical records: This species was reported from "Dévény" (= Devín village, Slovakia) already in the protologue of Jávorka (1915). Since then, this species was recorded repeatedly in this area, namely, from the vicinity of Devínska Kobyla hill near the city of Bratislava (e.g. Jávorka 1924, Domin & Podpěra 1928, Klika 1937, Dostál 1948, 1989, Kárpáti 1960, Májovský 1992, Feráková & Kocianová 1997). Kárpáti (1960), Kutzelnigg (1995) and Fischer et al. (2005) briefly mention the occurrence of this species in the Austrian part of the area studied, while Jakubowsky (1996) describe its regional distribution in detail. The oldest known herbarium specimen is from the Devínska Kobyla hill and dates from 1909 (leg. K. Ronniger, W). The name sometimes previously used for this taxon in the Malé Karpaty Mts was *Sorbus cretica* (Klika 1937, Dostál 1948, Kárpáti 1960).

Distribution and population size: *Sorbus danubialis* only occurs in the southern part of the mountain range. In Slovakia, it grows on Devínska Kobyla hill and in its surround-

ings. In Austria, it is scattered from Steinberg (Jakubowsky 1996) and Spitzeberg hills in the south to Braunsberg hill in the north. The centre of its distribution is located in the southern parts of the Hundsheimer Berg and Pfaffenberg hills. The occurrence of this species in the Malé Karpaty Mts is part of its rare to scattered distribution in suitable habitats in the adjacent regions of Austria, Moravia and Hungary (Kaplan et al. 2016, Kurtto et al. 2018). Similar to *S. collina*, its occurrence on Devínska Kobyla hill is at the northern limit of the distribution of this species. The size of the population in the area studied is estimated to be two hundred individuals.

Sorbus petraea Velebil, M. Lepší et P. Lepší, **spec. nova** (Figs 5–6; Supplementary Figs S4–S9).

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 glabrescent margins. Leaves on short sterile shoots simple; laminas broadly elliptical or rounded rhombic to almost rotund, (6.8–) 8.2–9.1 (–9.8) cm long and (5.4–) 6.9–7.6 (–9.0) cm wide, (1.1–) 1.2 (–1.3) times as long as wide, widest at (45–) 48–53 (–56) % of the lamina length (from the base), with obtuse apex with an angle of (120–) 130–140 (–145)°, broadly cuneate and partly serrate at base, with angle at base of (100–) 105–120 (–130)°, flat or slightly undulate at margins, finely, sharply double to triple serrate (rarely shallowly lobed), with more or less acute teeth terminating the main veins (other teeth ± equal), with (5–) 6–8 (–9) teeth between the 2nd and 3rd main vein from the base, with angle of the teeth terminating the 3rd main vein (35–) 45–55 (–65)°, with incision between the 2nd and the 3rd main vein from the base (3.0–) 3.4–4.6 (–5.6) mm, leathery, ± glossy, green, sparsely tomentose when young, later glabrescent on upper surface, evenly greenish grey- tomentose on lower surface, with (9–) 10 (–11) veins on each side, with the 3rd vein at an angle of (30–) 35–40° to midrib; petioles (9–) 11–12 (–13) mm long, tomentose. Leaf laminas on short fertile shoots similar in shape and size and more distinctly undulate at margin, almost rotund and usually rounded at base. 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 (6.9–) 7.5–8.2 (–9.1) mm long and (5.0–) 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 ~20; anthers pale yellow. Ovary semi-inferior. Styles 2, free or connate and tomentose at base. Fruit sub-globose, (12.5–) 13.5–14.5 (–15.0) mm long and (13.5–) 14.5–15.0 (–16.5) mm wide, wider than long or less often as wide as long, red at maturity, tomentose at top and base, otherwise glabrescent, matt, with (1–) 3–4 (–9) lenticels per 25 mm^2; mesocarp heterogeneous; endocarp cartilaginous. Seeds fuscous. DNA ploidy level: tetraploid (2n = 68, inferred using FCM). Reproduction mostly apomictic. Flowering in May.

Holotype: western Slovakia, Kuchyňa (distr. Malacky), Tri stodôlky rock ridge ~1.1 km N of summit of Vysoká hill, limestone rock, scattered, tree ~10 m high, 48°25'35.0"N, 17°12'53.8"E, 470 m a.s.l., 29 VIII 2018 leg. J. Velebil, M. Lepší & P. Lepší, CB 85684. – Isotypes: BRA (85684b), PR (85684a).

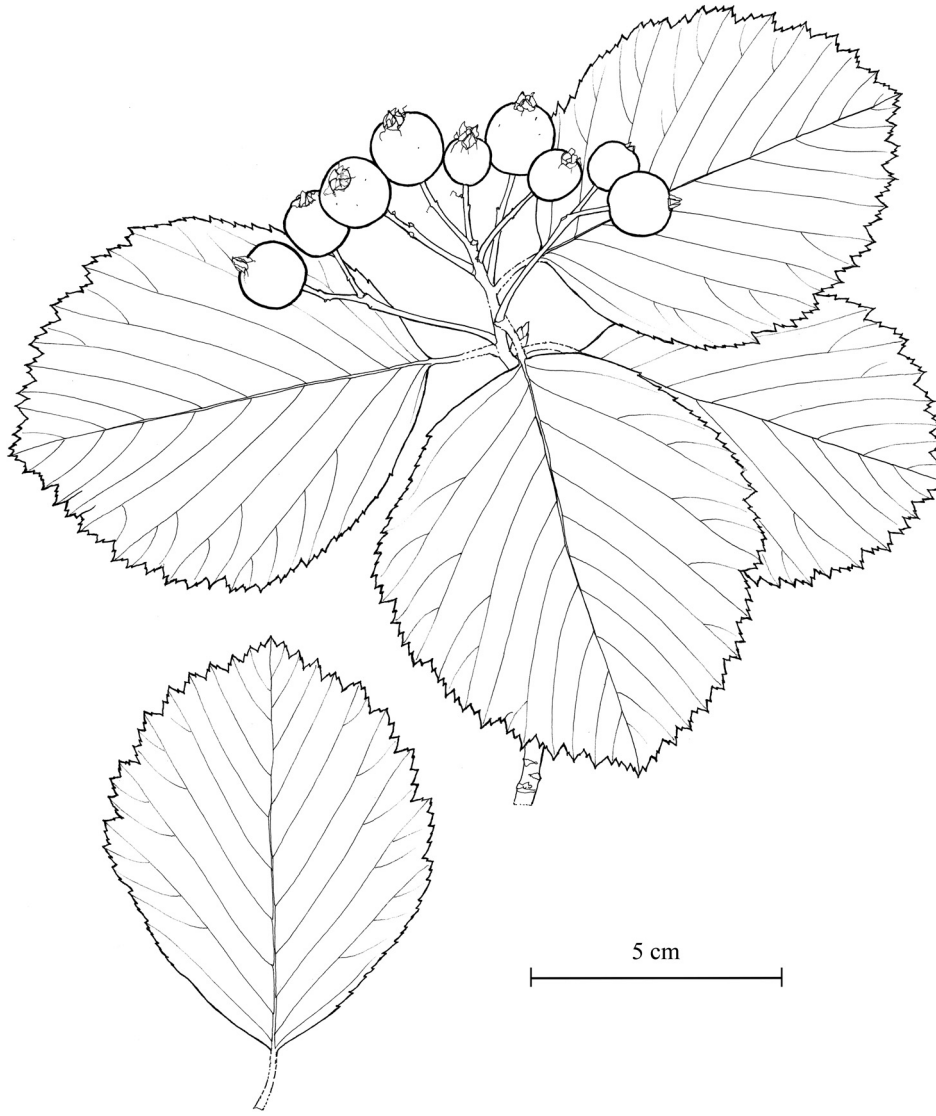

Fig. 5. *Sorbus petraea*: short fructiferous shoot (top) and leaf from the middle part of a short sterile shoot (bottom). Drawn by A. Skoumalová.

Diagnostic characters: Leaf laminas on short sterile shoots broadly elliptical or rounded rhombic to almost rotund, with obtuse apex, broadly cuneate at base, flat or slightly undulate at margins, finely, sharply double to triple serrate (rarely shallowly lobed), leathery. Petioles only (9–) 11–12 (–13) mm long. Leaf laminas on short fertile shoots more distinctly undulate at margin, almost rotund and usually rounded at base. Flowers relatively large. Fruit sub-globose, wider than long or less often as wide as long, red, only with (1–) 3–4 (–9) lenticels per 25 mm^2.

Fig. 6. Holotype of *Sorbus petraea*.

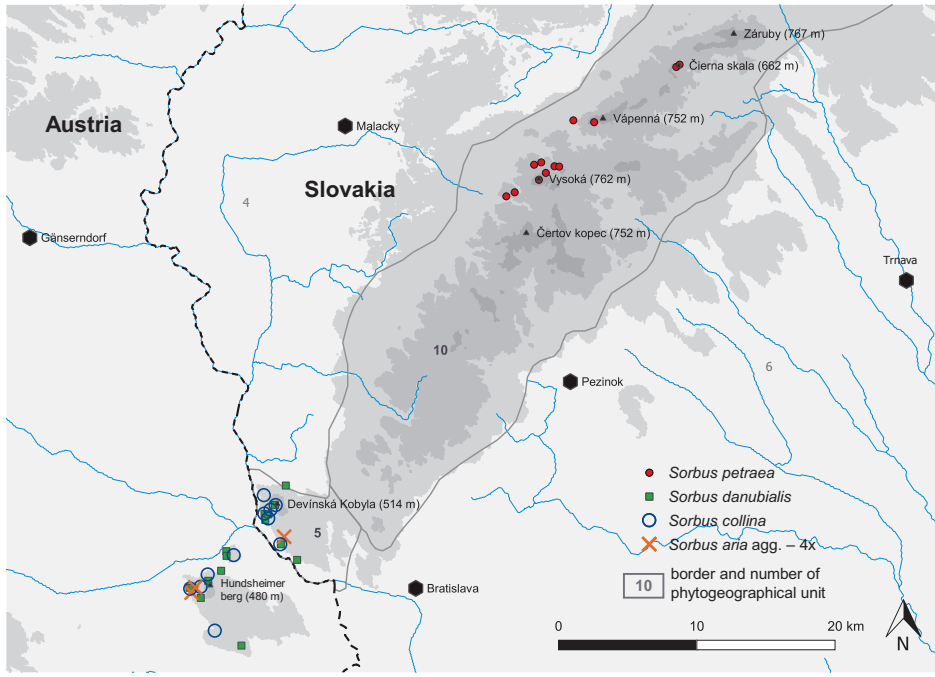

Fig. 7. Map showing the distribution of tertaploid taxa of *Sorbus* subgen. *Aria* in the Malé Karpaty Mts based on localities documented by herbarium specimens. The names of phytogeographical units in Slovakia are: 4 – Záhorská nížina, 5 – Devínska Kobyla, 6 – Podunajská nížina, 10 – Malé Karpaty (Futák 1984). Map source: EEA (2012), OpenStreetMap (2014), Eurostat (2020), Jarvis et al. (2008).

Taxonomy and similar species: The most similar species to *Sorbus petraea* in the area studied are *S. collina* and *S. danubialis*. Both of them differ in having longer petioles, less deeply and less sharply serrated margins of leaf laminas and smaller angles of laminar bases. *Sorbus collina* also has a longer leaf lamina, and *S. danubialis* is distinguished by a leaf lamina, which is often laterally asymmetrical, roughly serrated or irregularly lobate apically with noticeably undulated margins. Another similar taxon is the tetraploid species *S. thayensis*, endemic to the Podyjí region in the Czech Republic and Austria. It differs in having longer and more finely and sharply serrated leaf laminas and fruit ellipsoid to sub-globose, never wider than long. Other similar tetraploid taxa are *S. thaiszii*, known from eastern Slovakia (Gömör-Torna Karst) and *S. zolyomii*, occuring in north-eastern Hungary (Mátra and Bükk Mts). *Sorbus thaiszii* differs in having longer petioles and leaf laminas on fertile shoots, which are widest at the base. *Sorbus zolyomii* is distinguished by a longer petiole, larger leaf laminas with more, (9–) 10–11 (–12), veins and a distinctly triangular (acute) apex.

Etymology: The epithet "*petraea*" refers to the characteristic habitat of the species: rocks. We propose the name "jarabina skalná" for the Slovak name.

Ecology: *Sorbus petraea* exclusively inhabits limestone and dolomite treeless rocks and rocky ridges that usually rise from summits of densely beech-wooded hills. The species usually grows on the upper parts of rocky outcrops covered with sparse forestless

vegetation. This vegetation has a relict character and hosts many rare and endangered non-forest plants. *Sorbus petraea* is shadow-intolerant and dies when overshadowed by other species of trees. The species grows sympatrically with *S. aria* and is also recorded at the same locality with two singular triploids of the *S.* subgen. *Aria* that could be products of hybridization of *S. petraea* and *S. aria*. In close vicinity of its populations, two species of other subgenera also occur: *S. torminalis*, a member of the *S.* subgen. *Torminaria*, and, very rarely, *S. aucuparia*, a member of the *S.* subgen. *Sorbus*.

Genetic variation: The genetic variation of *Sorbus petraea* is low and does not correlate with geography, indicating a monotopic origin for this species. A similar level of variability is reported in other agamospermous *Sorbus* taxa and is usually attributed to random mutations (Lepší et al. 2008, 2009, Vít et al. 2012). While intraspecific variation is low, the genetic differentiation of this species from other taxa analysed is distinct. Both these observations support the independent status of this endemic *Sorbus* species as a unique evolutionary unit and justify its recognition at the species level.

Historical records: This species was first collected by Jasičová, Hubová and Zahradníková on rocks between Malá Vápenná hill and Vápenná Mt. in 1961 (SAV) and subsequently at approximately the same locality by Žertová in 1963 (PR). The third and fourth known herbarium vouchers were collected by T. Králik in 1997 and 1999 (SLO). The last remarkable specimen stored in W and collected by Wiesbaur from Vysoká Mt. in 1867 contains only one well-developed leaf on a short fertile shoot; therefore, it is not sufficient for safe determination, and for this reason, we do not include it in the list of herbarium specimens (Supplementary Data S1).

Distribution and population size: *Sorbus petraea* is a steno endemic recently confirmed occurring in two areas in the central part of the Malé Karpaty Mts, which are 15.7 km apart (Fig. 7). The first area is located in the vicinity of Vysoká Mt. near the village Kuchyňa (distr. Malacky), where approximately 70 individuals of various ages occur at five localities. The distance between the north-easternmost locality on Horný vrch hill and the south-westernmost occurrence on the south-east slope of Modranská skala rock is approximately 4.2 km. The largest population, consisting of approximately 35 individuals, is located on the Tri stodôlky rocks of a hill east of Zámok hill and smaller populations of approximately 20 individuals are on Vysoká Mt. At other localities (Bartalová hill, Horný vrch hill and Modranská skala rock) there are only one to ten individuals. The second and smaller area with an occurrence of *S. petraea* is situated on Čierna skala hill by the village Plavecký Mikuláš (Malacky distr.). It consists of approximately 30 shrubby individuals occurring on a rocky ridge that is approximately 300 m long. The third known but historical site with occurrence of this species is situated in the surroundings of Vápenná Mt., which lies between the two above mentioned localities. This occurrence is documented by herbarium specimens only and was not confirmed by our field survey. The altitudinal range of the species spans from 350 m (slopes of Modranská skala rock) to approximately 700 m a.s.l. (Vysoká and Vápenná Mts). All localities are situated in the phytogeographical district of Malé Karpaty (Futák 1984). Despite the very detailed field observation of the suitable habitats within the whole mountain range, no other locality of *S. petraea* was found. The most detailed exploration was conducted at the following localities: Bačkorová hill, Ražňová hill, Ostrý vrch hill, Pristodolok hill, Taricové skaly rocks, Biela skala hill, Jelenec hill, Geldek hill, Mesačná hill, west rocky ridge of Dlhý vrch hill, Malá Vápenná hill, Vápenná Mt., Kamenná hill, Klokoč hill, Pohanská hill,

Kršlenica hill and connected rocky ridge, Jelenia hora hill, Záruby Mt. and connected mountain ridge with the ruin of Ostrý kameň castle, Veterlín Mt., Čelo Mt., Smolenice karst by the village of Smolenice and Holý vrch hill by Horné Orešany.

Conservation: All localities are in the Malé Karpaty Protected Landscape Area. This species (number of individuals is estimated at 100) should be included among the critically endangered plants in the Slovak flora (CR; sensu Eliáš et al. 2015) and critically endangered species [status criteria B2ab(iv,v); Ca(i)] according to the IUCN (2012).

Single tetraploids

We sampled three tetraploid individuals of *Sorbus* subgen. *Aria* that do not meet the morphological and microsatellite patterns of any of the three recognized tetraploid taxa in the region. They were sampled at two sites in the Hainburger Berge hills and one locality in the Fialková dolina gorge. They show unique molecular patterns that indicate that they are of independent origin. The sample from Pfaffenberg hill occupies an intermediate position between *S. collina* and *S. aria* in the PCoA graph, indicating that it is probably a result of hybridization between these two species (Fig. 1). The two remaining samples are close to the group of *S. aria*, and thus their second parent is unclear. Based on morphology, Jakubowsky (1996) reports rare occurrences of transitional taxa between *S. danubialis* and *S. graeca* from the Austrian part of the area studied (Hexenberg hill). These records could relate to some of the above-mentioned single tetraploid or triploid individuals.

Unclear and mistakenly reported taxa

Sorbus austriaca (Beck) Hayek, Sched. Fl. Stir. Exs. 3: 9. 1905.

Lectotype designated by M. Lepší (in Sennikov & Kurtto 2017): Austria, Niederösterreich, Im Rettenbachgraben bei Prein, 5 VIII 1882 leg. G. Beck, PRC 455074. – Isolectotype: PRC 455073.

Sorbus austriaca is a member of the hybridogenous *S*. subgen. *Soraria* originating from crossbreeding between *S*. subgen. *Aria* and *S*. subgen. *Sorbus*. This species was described from the Austrian Alps (Beck 1892), is tetraploid (Lepší et al. 2015) and is reported many times from the Malé Karpaty Mts in the past (e.g. Domin & Podpěra 1928, Klika 1936, Dostál 1948, 1989, Májovský & Uhríková 1990, Májovský 1992, Marhold et al. 2007); however, all these records are very likely for deeply lobed morphotypes of diploid *S. aria.* This is based on the following reasons. First, we did not find any member of *S*. subgen. *Soraria* in the area studied, and second, all lobed individuals sampled resembling *S. austriaca* were diploids and fit morphologically and genetically in *S. aria*. Similarly, most records of *S. austriaca* from the Czech Republic are based on misidentification of lobed individuals of *S. aria* (Lepší et al. 2011, 2015). Finally, based on the revision of herbarium material we found that the record of the occurrence of diploid *S. austriaca* in the area studied (Májovský & Uhríková 1990, Marhold et al. 2007) applies in fact to *S. aria*. In conclusion, *Sorbus austriaca* does not, to our knowledge, occur in the Malé Karpaty Mts.

Sorbus buekkensis (Soó) Soó in Jávorka & Soó, A magyar növényvilág kézikönyve 1: 248. 1951.

Type is not designated. We refrain from designating a lectotype because the search for the original material and investigation of the type locality continues.

The origin, circumscription and distribution of *Sorbus buekkensis* are unclear and need to be clarified (Kurtto et al. 2018). This species was originally described from the Bükk Mts as a subspecies of *S. aria* (Soó 1937), but at present, some authors have included this species in hybridogenous *S.* subgen. *Soraria* based only on leaf morphology and without any support from laboratory methods (Sennikov & Kurtto 2017, Kurtto et al. 2018). There is only one record of the occurrence of this species in the area studied, which is located in the Hrabutnica gorge in the Čachtice Hills, in the northernmost part of the Malé Karpaty Mts (Kovanda 1961). However, the author considers *S. buekkensis* to be an unstable form of *S. aria*. Taking this and our field and laboratory investigations into account, we suppose that this record relates to the morphologically variable species *S. aria*.

Sorbus carpatica (Soó) Kárpáti, Borbásia Nova 25: unnumbered page. 1944, nom. illeg., non Andrz. 1845 (Art. 53.1., Turland et al. 2018).

In the area studied, the name *Sorbus carpatica* was used for morphotypes of the *S.* subgen. *Aria* with shallowly lobed leaves that were believed to have originated from a crossing between *S. aria* and *S. austriaca* (Kárpáti 1960, Dostál 1989, Májovský 1992, Jakubowsky 1996). The results of our field and laboratory investigation showed that these records actually refer to lobed forms of *S. aria*. The same applies for herbarium specimens identified as *S. carpatica* in SLO and referred to in Májovský & Uhríková (1990) and Marhold et al. (2007). In a similar way, all records of *S. carpatica* from the Czech Republic were based on misidentification of lobed individuals of *S. aria* (Lepší et al. 2015).

Sorbus graeca (Spach) Schauer, Übers. Arbeiten Veränd. Schles. Ges. Vaterl. Cult. 1847: 292. 1848.

Lectotype designated by Aldasoro et al. (2004): Turkey. “Ex monte Ida”, Herb. Tournefort 6150, P P00680357.

At present, the name *Sorbus graeca* s.l. is probably used for an artificial assemblage of related taxa occurring in central and southern Europe (Sennikov & Kurtto 2017, Kurtto et al. 2018). Most of the records of *S. graeca* from the Malé Karpaty Mts (Dostál 1989, Májovský 1992, Jakubowsky 1996, Feráková & Kociánová 1997, Kurtto et al. 2018) refer in reality to *S. collina* or possibly also to *S. petraea*. Some *S. graeca* records from Hainburger Berge hills (Jakubowsky 1996) probably relate to other single polyploids that we documented as scattered in the mountain range studied (see above).

Sorbus pannonica Kárpáti, Borbásia Nova 25: 10. 1944.

Lectotype designated by Somlyay & Sennikov (2015): Hungary, Bakony Mts, Isztimér, ”Burok-völgy”, 24 V 1936 leg. L. Vajda, BP 390405.

Sorbus pannonica is a triploid species confined to the Vértes Mts, eastern Bakony Mts and eastern Balaton Uplands in Hungary. All reports from other countries are most likely erroneous and refer to other members of *S.* subgen. *Aria* (Somlyay & Sennikov 2015). According to our results, this also applies to the records from the Malé Karpaty Mts

(Kárpáti 1960, Dostál 1989, Májovský 1992), where no triploid *Sorbus* that resembled *S. pannonica* was recorded.

Sorbus thaiszii (Soó) Kárpáti, Borbásia Nova 25: unnumbered page. 1944.

≡ *Sorbus aria* f. *thaiszii* Soó, Tisia 2: 223. 1937. – **Lectotype (designated here):** Slovakia, Gömör-Torna Karst, Jasov (Jászó), Hámorka hill (Szépleány-hegy), 10 VI 1909 leg. L. Thaisz, BP 219595, as "*Sorbus aria* (L.) Cr. pr. *cyclophylla* (Beck) m.", with a revision label by S. Jávorka (June 1915) as "*S. cretica* f. *danubialis* Jáv. in *S. ariam* transiens", and with a note written by Soó in pencil: "f. *Thaiszii* Soó", another revision label by L. Felföldy (20 March 2006) with determination "*Sorbus thaiszii* (Soó) Kárp." and an information label by L. Somlyay (April 2011) affiliated the specimen to the type material (Supplementary Fig. S10). **Epitype (designated here):** eastern Slovakia, Jasov (Košice-okolie distr.), Jasovská skala, ~560 m SW of cemetery church in village, rocky scrub on upper edge of rock, 330 m a.s.l., 48°40'42.35"N, 20°58'21.54"E, scattered, shrub ~4 m high, 21 VII 2020 leg. M. Lepší & J. Velebil, CB 86866, Supplementary Fig. S11. – Isoepitypes: BP (86866a), BRA (86866b), PR (86866c), PRA (86866e), W (86866d).

The original material consists of a drawing of a leaf (Soó 1937: 221, table II, fig. 11) and four herbarium specimens from three localities cited in the protologue and today preserved in BP. The first specimen comes from Szépleány hill (Hámorka hill) on the south-west edge of the village of Jasov (Jászó) ("Hung. bor. Com. Abauj-Torna. In monte Szépleány, ad pagum Jászó.", 10 VI 1909 leg. L. Thaisz, BP 219595), the second and third from Jelení vrch hill (Szarvas-hegy) north of the village of Hačava (Falucska) ("Hung. bor. Com. Abauj-Torna. In monte Szarvashegy, supra pagum Falucska.", 14 VIII 1909 leg. L. Thaisz, BP 219596, BP 712064). The fourth specimen probably comes from the surroundings of the village of Jovice (Jólesz) near the town of Rožňava (Rozsnyó), but we were not able to trace the exact location of the site ("Comit. Gömör. In monte Jóleszi hegy ad Rozsnyó.", 23 V 1911 leg. A. Degen, BP 219594). We designated the specimens from the surroundings of Jasov as a lectotype (Supplementary Fig. S10), because the drawing given in the protologue was drawn based on a plant coming from this locality, as explicitly stated there. This decision was based on the fact that the species was recently abundant in the surroundings of this locality and the only tetraploid recorded there (tested by flow cytometry and molecular analyses). Moreover, the uniform morphology of this population corresponds morphologically with the current concept of the species (Németh 2009). As tetraploid *Sorbus* are quite taxonomically complex in this region and the lectotype does not include the sterile shoots necessary for a safe determination, we selected the interpretative type from the original locality.

Sorbus thaiszii is currently reported from south-eastern Slovakia and adjacent Hungary (Kurtto et al. 2018). In the protologue of the name, it was initially reported only from Gömör-Torna Karst (Soó 1937), and later, Kárpáti (1960) added records from Hungary and the Austrian part of the Malé Karpaty Mts; Wolfstal: Leányvár-Berg (ruin of Pottenburg near Wolfsthal). Jakubowsky (1996) also reports this species from Hainburger Berge hills (Braunsberg and Königswarte hills) and considers it to be a transitional form between *S. aria* and *S. graeca* in line with some other authors (Májovský 1992). Our field and herbarium investigation and molecular data show that *S. thaszii* does not occur in the area studied and should be deleted from the regional checklist.

Sorbus zolyomii (Soó) Kárpáti, Borbásia Nova 25: unnumbered page. 1944.

≡ *Sorbus aria* f. *zolyomii* Soó in Tisia 2: 220. 1937. – **Lectotype (designated here by L. Somlyay):** Hungary, Heves county (Comit. Heves), Pétervására distr., Parád; "In rupestribus andesiticis montis Saskő pr. Parádfürdő", 29 VII 1928 leg. Á. Boros, BP 712065, as "*Sorbus*", with a revision label by Soó (without date) as "*S. aria* ssp. *cyclophylla* (Beck) f. *Zólyomii* Soó", with an information label by L. Somlyay (November 2011) affiliated the specimen to the original material and his later revision label (May 2016) with determination "*Sorbus zolyomii* (Soó) Kárpáti" (Supplementary Fig. S12). Isolectotype: BP 432321. **Epitype (designated here):** Northern Hungary, Parád (Pétervására distr.), ~240 m WNW of summit of Kis-Saskő hill, rock, 860 m a.s.l., 47°52'25.0"N, 20°1'49.19"E, scattered, shrub ca 5 m high, 20 VII 2020 leg. J. Velebil & M. Lepší, CB 86857, Supplementary Fig. S13. – Isoepitypes: BP, 86857a; BRA, 86857b; PR, 86857c; PRA, 86857e; W, 86857d.

In the protologue, the taxon is reported from several remote regions in Hungary and Slovakia (Soó 1937), which in itself raises the suspicion that the taxon is broadly defined. Indeed, our comparative study of original material (BP 712065, BP 595178, BP 388983, BP 432331, BP 432321, BP 432319, BP 432318) showed that the taxon in the original concept includes several taxa or morphotypes. The most important part of the original material is specimen BP 712065 collected by Á. Boros on the "Sas-kő" ridge (Mátra Mts, northern Hungary) on 29 July 1928 (Supplementary Fig. S12) accompanied by the identification label written by Soó. It was used (specifically its the left most leaf) as a template for the illustration in the protologue (Soó 1937: 219, table I., fig. 9). This specimen was treated as a representative of *Sorbus zolyomii* by Soó (1937) and subsequently by Kárpáti (1960); thus, it serves as the basis for the interpretations of this name. To fix the application of the name *S. zolyomii*, this specimen is designated here as the lectotype of this name. As the lectotype and its duplicate (BP 432321) contain sterile shoots grown in shade, as evident from the note Á. Boros attached to the latter specimen, we interpret the lectotype by selecting an epitype originating from the original locality. The population of *S. zolyomii* at Sas-kő is vigorous and consists of at least 20 tetraploid and morphologically uniform individuals, which indicates an apomictic mode of reproduction and stable population. Moreover, our field observations and molecular analyses confirmed the occurrence of this taxon at Mt. Bél-kő in the Bükk Mts, a locality cited in the protologue, which is 31 km distant from Sas-kő. The unpublished preliminary results of L. Somlyay and his coworkers also indicate that *S. zolyomii* is widely distributed in both the Mátra and Bükk Mts. In conclusion, *S. zolyomii* is a clearly defined tetraploid and presumably apomictic species related to *S. danubialis*, occurring in northern Hungary (Mátra and Bükk Mts). The recently published range of distribution of this species (Kurtto et al. 2018) is probably overestimated, and the distribution map apparently also includes other taxa. At least the plant from the Malé Karpaty Mts reported in the protologue for this species (Soó 1937, "Comit. Pozsony. In calcareis montis Rachsthurn prope Széleskut" [= Vápenná Mt. near Sološnica]), based on the specimen collected by Á Boros (BP 432319), unambiguously does not belong to *S. zolyomii*, but to a different member of the *S.* subgen. *Aria*. The report of the occurrence of this species in Čachtice Hills (Kovanda 1961) also does not apply to *S. zolyomii*, but to some form of *S. aria*. This conclusion stems from our

field and herbarium survey, which did not find any polyploid member of *S*. subgen. *Aria* in this part of the mountain range.

Key for identification of the species of *Sorbus* subgen. *Aria* occurring in the Malé Karpaty Mts

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

1b Leaf lamina more or less stiff, smaller, (6.5–) 7.5–9.9 (–12.5) cm long, within population uniform, broadly elliptical or rounded rhombic to almost rotund, veins on each side (8–) 9–10 (–11) 2

2a Leaf lamina flat at margins, regularly simply or double (to triple) serrate, with incision between the 2nd and 3rd main veins from the base (1.3–) 1.8–2.8 (–3.7) mm, broadly elliptical to almost rotund, (8.4–) 9.0–9.9 (–12.5) cm long, with obtuse, rounded or truncate apex ..... ***S. collina***

2b Leaf lamina flat to undulate at margins, finely to coarsely unevenly double to triple serrate (rarely shallowly lobed), with incision between the 2nd and 3rd main veins from the base (1.7–) 2.7–4.6 (–5.6) mm, broadly elliptical or rounded rhombic to almost rotund, (6.5–) 7.4–9.1 (–10.8) cm long, with broadly acute to obtuse apex 3

3a Petiole (11–) 13–16 (–21) mm long, leaf lamina with incision between the 2nd and 3rd main veins from the base (1.7–) 2.7–3.4 (–4.5) mm, with angle of the teeth terminating the 3rd main veins (55–) 65–80 (–95)°, with angle at base of (75–) 90–105 (–120)°, leaf laminas on short fertile shoots rounded rhombic, less often broadly elliptical to almost rotund, broadly cuneate at base ..... ***S. danubialis***

3b Petiole (9–) 11–12 (–13) mm long, leaf lamina with incision between the 2nd and 3rd main veins from the base (3.0–) 3.4–4.6 (–5.6) mm, with angle of the teeth terminating the 3rd main veins (35–) 45–55 (–65)°, with angle at base of (100–) 105–120 (–130)°, leaf laminas on short fertile shoots almost rotund, usually rounded at base ..... ***S. petraea***

Supplementary materials

Fig. S1. – Representative herbarium specimen of *Sorbus aria* (L.) Crantz.
Fig. S2. – Representative herbarium specimen of *Sorbus collina* M. Lepší, P. Lepší et N. Mey.
Fig. S3. – Representative herbarium specimen of *Sorbus danubialis* (Jáv.) Prodan.
Fig. S4. – Short fertile shoot of *Sorbus petraea*.
Fig. S5. – Flowers of *Sorbus petraea*.
Fig. S6. – Habitus of *Sorbus petraea* growing on rocks.
Fig. S7. – Typical habitat of *Sorbus petraea*.
Fig. S8. – Typical habitat of *Sorbus petraea*.
Fig. S9. – Typical habitat of *Sorbus petraea*.
Fig. S10. – Lectotype of *Sorbus thaiszii* (Soó) Kárpáti.
Fig. S11. – Epitype of *Sorbus thaiszii* (Soó) Kárpáti.
Fig. S12. – Lectotype of *Sorbus zolyomii* (Soó) Kárpáti.
Fig. S13. – Epitype of *Sorbus zolyomii* (Soó) Kárpáti.
Table S1. – Locality details of populations of *Sorbus* subgen. *Aria* included in analyses.
Table S2. – Observed sample/standard ratio for each sample measured by flow cytometry, deduced DNA ploidy level and coefficients of variation for standard and sample.
Table S3. – Average values of sample/standard ratio and coefficients of variation measured by flow cytometry for each ploidy level.
Table S4. – Average values of sample/standard ratio, estimated ploidy level and coefficients of variation measured by flow cytometry for each taxon.
Data S1. – List of herbarium specimens studied.

Supplementary materials are available at www.preslia.cz

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Taxonomické zhodnocení *Sorbus* subgenus *Aria* v Malých Karpatech

V příspěvku jsou představeny výsledky taxonomické revize jeřábů z podrodu *Aria* (*Sorbus* subgen. *Aria*) v Malých Karpatech (západní Slovensko a severovýchodní Rakousko). K hodnocení taxonomické rozmanitosti této skupiny bylo využito podrobného terénního průzkumu, revize herbářových dokladů, mnohorozměrných morfometrických i molekulárních analýz (analýza mikrosatelitů) a průtokové cytometrie. Ve sledované oblasti byly zaznamenány diploidní, triploidní a tetraploidní jeřáby. Jediným zaznamenaným diploidním druhem je *S. aria*, který vykazuje značnou morfologickou a genetickou variabilitu. Ve studované oblasti roste vzácně, roztroušeně až místy hojně. Triploidní zástupci jsou svým výskytem omezeni na střední a jižní část regionu a zahrnují několik singulárních, pravděpodobně apomiktických, jedinců a vzácných apomiktických linií, které zde nejsou z důvodu velmi omezeného počtu zaznamenaných exemplářů hodnoceny jako samostatné druhy. Tetraploidní zástupci mají obdobné rozšíření jako zástupci triploidní. *Sorbus danubialis* a *S. collina* se vyskytují v jižní části pohoří, zatímco nově popsaný druh, *S. petraea* Velebil, M. Lepší et P. Lepší, osidluje střední část pohoří. Celá populace *S. petraea* čítá přibližně sto jedinců. Druh se vyskytuje hlavně v okolí hory Vysoká u obce Kuchyňa, kde vytváří několik mikropopulací, a na vrchu Čierna skala u obce Plavecký Mikuláš, kde roste asi 30 jedinců. Kromě těchto recentních lokalit existují i starší herbářové doklady z 60. let 20. století dokumentující výskyt druhu z hory Vápenná u Sološnice. Nízká genetická a morfologická variabilita druhu, stejně jako způsob rozmnožování testovaný pomocí průtokové cytometrie semen, dokládají apomiktický způsob rozmnožování a opravňují hodnocení *S. petraea* jako samostatného druhu. Oprávněnost hodnocení na úrovni druhu potvrdily všechny použité biosystematické metody, které ukázaly, že se *S. petraea* významně morfologicky a geneticky liší od příbuzných tetraploidních druhů *S. danubialis* a *S. collina*. *Sorbus collina* je v tomto příspěvku poprvé uveden pro flóru Slovenska. Dříve uváděné druhy *S. austriaca*, *S. buekkensis*, *S. carpatica*, *S. graeca*, *S. pannonica*, *S. thaiszii* a *S. zolyomii* nebyly ve sledovaném území potvrzeny a příslušné údaje jsou zde proto považovány za mylné. Pro druhy *S. thaiszii* a *S. zolyomii* jsou stanoveny nomenklatorické typy. Příspěvek rovněž přináší určovací klíč, podrobné mapy rozšíření a fotografie reprezentativních herbářových položek všech taxonů studovaného podrodu jeřábů vyskytující se v pohoří Malé Karpaty. Publikována je také perokresba a fotografie nově popisovaného druhu.

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