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CONTENTS

Modern Phytomorphology **9** (**Suppl.**): 5–15, 2016

TWO MAJOR GROUPS OF CHLOROPLAST DNA HAPLOTYPES IN DIPLOID AND TETRAPLOID *ACONITUM* SUBGEN. *ACONITUM* (RANUNCULACEAE) IN THE CARPATHIANS

J. Mitka [1]*, P. Boroń [2], A. Novikoff [3], A. Wróblewska [4], B. Binkiewicz [1]

Abstract. *Aconitum* in Europe is represented by ca. 10% of the total number of species and the Carpathian Mts. are the center of the genus variability in the subcontinent. We studied the chloroplast DNA intergenic spacer *trn*L$^{(UAG)}$-*rpl*32-*ndh*F (cpDNA) variability of the *Aconitum* subgen. *Aconitum* in the Carpathians: diploids (2n=16, sect. *Cammarum*), tetraploids (2n=32, sect. *Aconitum*) and triploids (2n=24, nothosect. *Acomarum*). Altogether 25 *Aconitum* accessions representing the whole taxonomic variability of the subgenus were sequenced and subjected to phylogenetic analyses. Both parsimony, Bayesian and character network analyses showed the two distinct types of the cpDNA chloroplast, one typical of the diploid and the second of the tetraploid groups. Some specimens had identical cpDNA sequences (haplotypes) and scattered across the whole mountain arch. In the sect. *Aconitum* 9 specimens shared one haplotype, while in the sect. *Camarum* one haplotype represents 4 accessions and the second – 5 accessions. The diploids and tetraploids were diverged by 6 mutations, while the intrasectional variability amounted maximally to 3 polymorphisms. Taking into consideration different types of cpDNA haplotypes and ecological profiles of the sections (tetraploids – high-mountain species, diploids – species from forest montane belt) we speculate on the different and independent history of the sections in the Carpathians.

Key words: *Aconitum,* Carpathian Mts., cpDNA haplotypes, ploidy levels

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Introduction

The genus *Aconitum* L. comprises approximately 300 species distributed in temperate regions of the N Hemisphere, mostly in eastern Asia (Kadota 1987; Liangqian & Kadota 2001). The subgenus *Aconitum* contains ca. 250 species and around 10% of them can be found in Europe, mainly in the mountain areas (Götz 1967; Seitz 1969). The subgenus *Aconitum* in Europe consists of the sect. *Aconitum*, sect. *Cammarum* DC. and nothosect. *Acomarum* Starmühl. (Starmühler 2001; Mitka 2003). This division goes along ploidy level, where sect. *Cammarum* represents diploids (2n=16) and sect. *Aconitum* – tetraploids (2n=32), while hybridogenic nothosect. *Acomarum* contains plants with 2n=24 (Joachimiak *et al.* 1999; Mitka *et al.* 2007; Ilnicki & Mitka 2009, 2011).

These sections in Europe differ not only morphologically and cytogenetically but also ecologically (Novikoff & Mitka 2011, 2015). Diploids are the lowland and montane-zone species (up to ca. 1150 m above sea level), and tetraploids are high-mountain species found predominantly in the subalpine and alpine zones. Triploids have intermediate position but mostly prefer lower altitudes and open habitats. Generally, diploids are forest and tetraploids an open mountainous area species growing above the upper forest line (Joachimiak *et al.* 1999; Mitka 2003; Novikoff & Mitka 2011).

The aim of this study was to check variability of chloroplast DNA (cpDNA haplotypes) in the sections *Aconitum* and *Cammarum* in the Carpathians. cpDNA is thought to be slowly evolving and thus useful in the phylogenetic reconstructions of the higher taxonomic levels

(Avise 2004). The species are the Carpathian endemics but *A. variegatum* being a European endemic and *A. toxicum* distributed also in the Balkans. Isolated position of the mountain range and high endemicity makes it a promising object of the phylogeographic investigations.

The background hypothesis concerns the origin of the tetraploids in the Carpathians. If they originated directly from the local diploid stock they should share a great deal of the variability. If diploids and tetraploids harbor distinctly different cpDNA haplotypes it can mean that they originated in the mountain range by independent migrations. To check the hypothesis we use maternally inherited *trn*L$^{(UAG)}$-*rpl*32-*ndh*F intergenic spacer sequences of cpDNA.

Material and methods

Sampling and DNA extraction and molecular techniques

25 accessions (Operational Taxonomic Units or OTUs) of *Aconitum* sect. *Aconitum* (ingroup) were sampled from the Carpathians (Tab. 1; Fig. 1). Two additional OTUs: *A. lycoctonum* L. em. Koelle and *A. moldavicum* Hacq. were set as an outgroup. The following species represent the whole taxonomical variability of the ingroup in the Carpathians: *A. degenii* Gáyer, *A. lasiocarpum* (Rchb.) Gáyer, *A.* ×*pawlowskii* Mitka & Starmühl., *A. toxicum* Rchb., and *A. variegatum* L. (diploids); *A. bucovinense* Zapał., *A.* ×*czarnohorense* (Zapał.) Mitka, *A. firmum* Rchb., and *A.* ×*nanum* (Baumg.) Simonk. (tetraploids). The ingroup encompasses additionally the two triploid (2n=24) hybrids found in the Carpathians: *A.* ×*cammarum* L. em. Fries (*A. napellus* × *A. variegatum*) and *A.* ×*berdaui* Zapał. (*A. firmum* × *A. variegatum*). Both of them are representatives of the nothosect. *Acomarum*. *A.* ×*cammarum* is an ornamental plants found in the rural gardens. The nomenclature of *Aconitum* follows www.ipni.org (see also Mitka 2003; Novikoff & Mitka 2011).

For all accessions either recently collected samples (stored as silica-dried leaves) or herbarium specimens were obtained. From this material samples for DNA extractions were prepared using ca. 2 cm^2 of fully developed leaf blade with no symptoms of damage caused by insects or fungal infections (Gawal & Jarret 1991). Samples were then grounded in 2 ml microcentrifuge tubes with 3 stainless steel beads (ø 3mm) by shaking in an oscillation mill (MM 200 – Retsch, Germany) for 4 minutes at 25Hz. Then, DNA was extracted separately for each sample with a Genomic Mini AX Plant DNA extraction kit (A&A Biotechnology, Poland), according to the manufacturer protocol.

The undiluted DNA extracts were used as templates in the amplification of the *trn*L$^{(UAG)}$-*ndh*F region of chloroplast DNA with primers *trn*L$^{(UAG)}$ – 5’-CTGCTTCCTAAGAGCAGCGT-3’ and *ndh*F – 5’-GAAAGGTATKATCCAYGMATATT-3’ (Shaw *et al.* 2007). The reaction was carried out in a total volume of 50 μl containing: 1× DreamTaq Green buffer (ThermoFisher Scientific), 3.5 mM MgCl$_2$, 0.08mM each of dNTPs, 0.08μM of both primers and 1u of DreamTaq DNA polymerase (ThermoFisher Scientific). Amplifications were run on a T100 Thermal Cycler (Bio-Rad) with the following temperature profile: 5 minutes of initial denaturation at 94°C; 25 touchdown cycles composed of 30 seconds at 94°C; 30 seconds at decreasing annealing temperatures (0.5°C/cycle from 67.5°C in the 1st to 55°C in the 25th cycle); 1 minute at 72°C; and 20 cycles of 30 seconds at 94°C, 30 seconds at 55°C, and 1 minute at 72°C; and 10 minutes at 72°C for the final extension step. The amplification effectiveness was verified by agarose gel electrophoresis, and positive PCR products were purified with the Clean-Up DNA purification kit (A&A Biotechnology, Poland). The purified PCR products were used as template in sequencing reaction.

Entire *trn*L$^{(UAG)}$-*ndh*F region was sequenced for all samples with use of PCR primers and set of internal sequencing primers: V1_F – 5’-AGGTTGAGTTATTGGTGGATGA-3’, V2_F – 5’-GTTCGCAAAGAACTGAAGTGAC-3’, V3_F – 5’-TGGATGATAGAATAYATATCAAAATCA-3’ (forward primers) and V2_R – 5’-TTTCCGGATTCACCAGCTCTT-3’, V3_R – 5’-CGAAAAGCCATTACATTCTTAAA-3’

Tab. 1. Localities of twenty five accessions of *Aconitum* subgen. *Aconitum* from the Carpathians (ingroup) and two accessions of an outgroup (*A. moldavicum* and *A. lycoctonum* from subgen. *Lycoctonum*). **JM** – J. Mitka; **MG** – M. Graniszewska; **PB** – P. Bochenek. Taxonomy follows Mitka (2003) and Novikoff & Mitka (2011).

Nr. of accession	Genus	species	subspecies	Region/Locality	Date of collection	Collector	Haplotype
001	*Aconitum*	×*cammarum*	-	W Carpathians/Vel'ká Fatra	27.07.2007	JM	C
003	*Aconitum*	*variegatum*	*variegatum*	W Carpathians/ Muranska planina	28.07.2007	JM	-
007	*Aconitum*	*degenii*	*degenii*	E Carpathians/Rodna	16.08.1998	JM	A
009	*Aconitum*	*firmum*	*maninense*	W Carpathians/Tatras	15.05.2008	JM	C
017	*Aconitum*	*toxicum*	*toxicum*	S Carpathians/Piatra Craiului	07.08.1999	PB	A
023	*Aconitum*	*firmum*	*maninense*	W Carpathians/ Stražovske vrchy	15.05.2008	JM	C
025	*Aconitum*	*bucovinense*	-	E Carpathians/Rarau	15.05.2008	JM	C
026	*Aconitum*	*variegatum*	*variegatum*	W Carpathians/Pieniny	26.08.2007	JM	B
029	*Aconitum*	*bucovinense*	-	Bihor/Cornul Muntilor	15.07.2006	JM	B
032	*Aconitum*	×*nanum*	-	S Carpathians/Fogaraš	15.05.2008	JM	-
033	*Aconitum*	*lasiocarpum*	*lasiocarpum*	E Carpathians/Ceahlău	08.08.2007	JM	-
034	*Aconitum*	*firmum*	*moravicum*	W Carpathians/W Beskyds	15.05.2008	JM	C
045	*Aconitum*	*degenii*	*degenii*	E Carpathians/Gorgany	11.08.2003	MG	A
047	*Aconitum*	*firmum*	*firmum*	W Carpathians/Tatras	27.08.2007	JM	C
048	*Aconitum*	×*czarnohorense*	-	E Carpathians/Rodna	15.08.1998	JM, PB	C
049	*Aconitum*	*toxicum*	*toxicum*	S Carpathians/Bucegi	07.08.1998	PB	A
054	*Aconitum*	*firmum*	*fissurae*	S Carpathians/Retezat	28.07.2007	JM	B
057	*Aconitum*	×*pawlowskii*	-	W Carpathians/Tatra	27.08.2007	JM	B
059	*Aconitum*	*lasiocarpum*	*kotulae*	W Carpathians/Nízke Tatra	19.08.2007	JM	-
062	*Aconitum*	*moldavicum*	*moldavicum*	Małopolska Upland/ Przeginia	26.07.2006	JM	-
063	*Aconitum*	*lycoctonum*	*lycoctonum*	Montenegro (Balkans)/ Durmitor	13.08.2009	JM	-
065	*Aconitum*	×*berdaui*	-	W Carpathians/Malá Fatra	31.07.2009	JM	-
066	*Aconitum*	*firmum*	*maninense*	W Carpathians/ Stražovske vrchy	01.08.2009	JM	C
072	*Aconitum*	*bucovinense*	-	E Carpathians/W Bieszczady	25.06.1996	JM	C
074	*Aconitum*	*bucovinense*	-	S Carpathians/Piatra Craiului	11.08.1999	JM	-
107	*Aconitum*	×*pawlowskii*	-	W Carpathians/ E Beskyds	24.08.2001	JM	A
50A	*Aconitum*	*degenii*	*degenii*	S Carpathians/Retezat	24.07.2009	JM	B

(revers primers) (Boroń *et al.* – unpublished). Sequencing was performed with a BigDye Terminator v.3.1 Cycle Sequencing Kit (Life technologies, USA) on a T100 thermal cycler (Bio-Rad) and a 3500 Series Genetic Analyzer (Life Technologies, USA) using standard protocols.

Phylogenetic analyses

The resulting sequences were processed and aligned with MEGA 6 software (Tamura *et al.* 2013). The alignment revealed the extensive length variation among sequences resulting from two types of length mutations, namely the indels and mononucleotide SSR loci. For our study we consider an indel all non-loci-specific gaps (all indels observed were at least 3 bp long safe for one 1 bp long indel). Similarly, all polynucleotide sites longer than 5 mononucleotide repeats for which length variation was observed were considered SSR loci. As the clear gaps' and SSR mutations' pattern were observed, these characters were encoded into two matrixes, i.e. binary (present vs. absent) gap matrix and standard characters (no. of mononucleotide repeats) SSR matrix. Than all sites with gaps were deleted from alignment as no point mutations were found for these regions. All three datasets, i.e. gap-free alignment, gap binary matrix and SSR standard matrix were combined into one datafile and analyzed simultaneously.

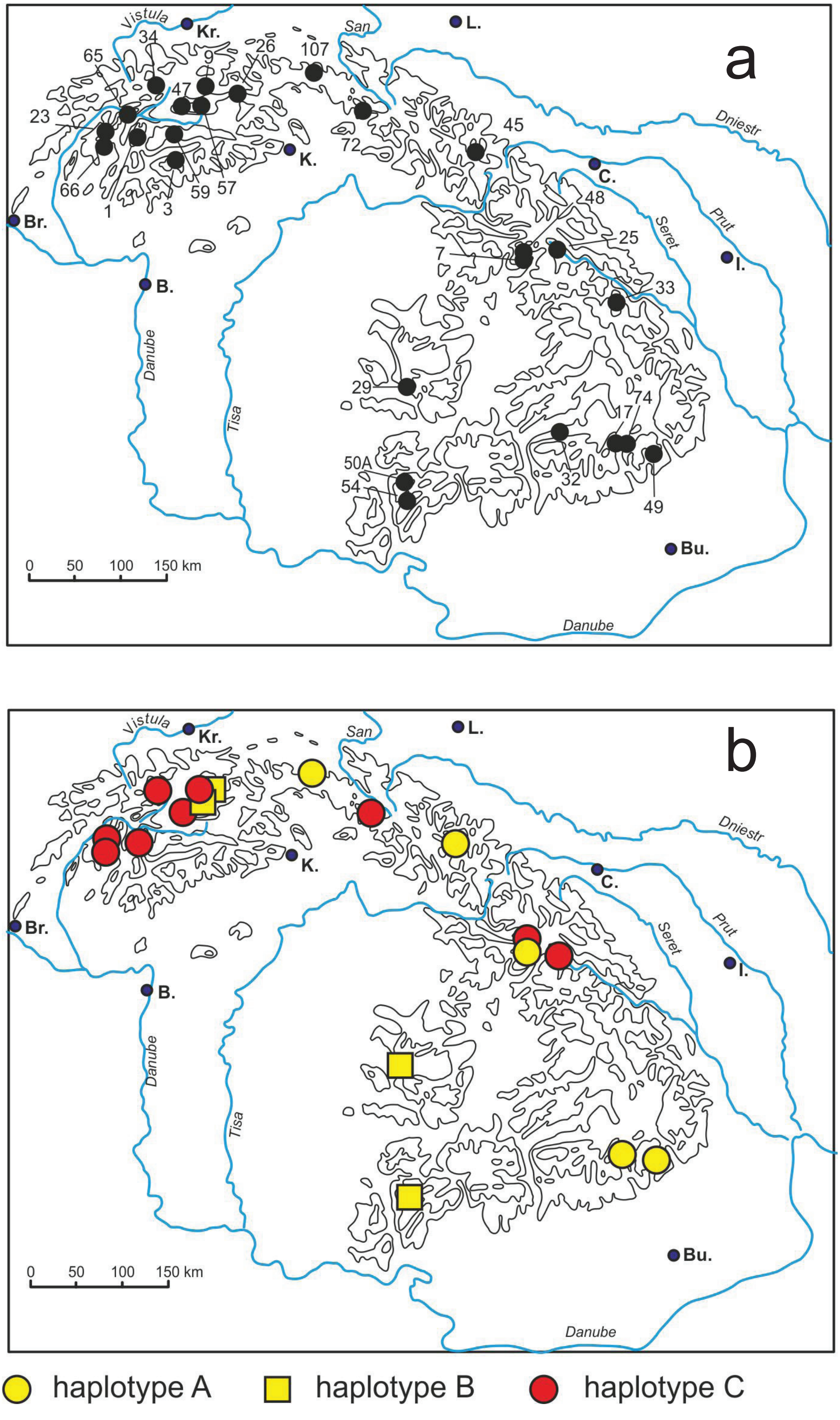
Restriction site data were analyzed using the maximal parsimony (MP) optimality criterion (Felsenstein 2004) using PAUP* (version 4.0.b10, Swofford 2002). Gaps were coded as a new character state. Insertions/deletions (indels) for which at least one sample exhibited polymorphism were coded as interleaved characters, and the corresponding nucleotide characters were excluded (Fergusson *et al.* 1999). Heuristic search was conducted with random addition, tree bisection-reconnection (TBR) branch swapping, and the MULTREES option on. The consistency index (CI; Kluge & Farris 1969), the retention index (RI), and rescaled consistency index (RC; Farris 1989a, 1989b) were calculated with PAUP*. Support for branches was evaluated by bootstrapping (BS; Felsenstein 2004). One thousand bootstrap replicates, each with 10 random stepwise additions were performed using the same settings as above and no more than 100 trees were retained per replicate.

A Bayesian Inference (Rannala & Yang 1996) implemented in the program MrBayes v. 3.1.2 (Huelsenbeck & Ronquist 2001) was used. In the analysis, two independent runs with four Markov chain Monte Carlo (MCMC) runs (three heated and one cold) were run simultaneously, sampling every 100 generations for 10 million generations and starting with a random tree. The first 2 million generations (25% of the total) were excluded as burning after convergence of the chains, which was evaluated by the average standard deviation of splitting frequencies reaching below 0.01. Gaps were coded in the matrix as presence/absence following the method proposed by Simmons & Ochoterena (2000) as implemented in SeqState (Müller 2005). Gaps were assumed to follow the binary model of evolution (Ronquist *et al.* 2005) and were included in the Bayesian analyses following Dwivedi & Gadagkar (2009).

A Minimum Spanning Network (MSN) were used to generate a distance graph with all of the edge sets of all minimum spanning trees (Huson & Bryant 2006) with the use of SplitsTrees software (www.splitstree.org). BS values were calculated based on 1000 replications.

The phylograms were edited in TreeView v.1.6.6 (http://taxonomy.zoology.gla.uc. uk/rod/htlm) and rooted with the two species of the subg. *Lycoctonum*: *A. lycoctonum* and *A. moldavicum*. If the genotypes of accessions were identical, only one of them was included in the analyses.

Fig. 1. Geographical distribution of sampled *Aconitum* subgen. *Aconitum* and haplotypes A, B, and C in the Carpathians. ► The numbers are concordant with those in Tab. 1. **Br** – Bratislava; **Bu** – Bucuresti; **B** – Budapest; **C** – Černivce; **I** – Jassy; **K** – Košice; **Kr** – Kraków; **L** – Lviv.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haplotype C

Results

The complete aligned *trn*L$^{(UAG)}$-*rpl*32-*ndh*F spacer was 996 bp long, 938 bp long after gaps and SSR loci were removed. The gap matrix consisted of 9 characters and SSR of 7 characters. 899 of the characters were constant, 10 variable characters were parsimony-uninformative and 29 characters were parsimony informative. Unweighted parsimony found 1 most parsimony tree of 47 steps, with a CI = 0.9362, RI = 0.9434, and RC = 0.8832. Analysis of the complete cpDNA restriction data set (25 + 2 outgroup OTUs) revealed the same sequences in some OTUs. Among diploids: OTUs no. 007, 017, 049, 057, and 107 (cpDNA haplotype A); 026, 029, 50A, and 057 (cpDNA haplotype B); and among tetraploids: 001, 009, 023, 025, 034, 047, 048, 066, and 072 (cpDNA haplotype C). They are distributed across the whole Carpathians (Fig. 1). The phylogenetic analyses were performed on the reduced data set, with only one representative of the each cpDNA haplotype A, B and C, i.e. with 10 (ingroup) and 2 outgroup accessions.

The differences among accessions within the diploids and tetraploids did not exceed 3 polymorphisms (substitutions and/or SSR mutations) and the differences between the diploids and tetraploids amounted to 6 steps (2 unique indels and 4 SSR mutations – Tab. 2; Fig. 2 c).

A Bayesian Inference (MrBayes) and MP (PAUP*) splits the OTUs into the diploid and tetraploid groups (Fig. 2 a, b). Both diploids and tetraploids had high support (0.99 posterior probability, PP and 61% BS). Among diploids *A. degenii* and *A. lasiocarpum* formed highly supported sister group (0.94 PP, 61% BS). The triploid *A.* ×*berdaui* joined with the diploids. The tetraploids: *A. firmum* subsp. *fissurae* and *A. bucovinense*, and the diploids: *A. degenii* and *A. lasiocarpum*, formed weakly (61% and 59% BS, respectively) supported sister groups.

The MSN clearly divides the *Aconitum* in the Carpathians into the two ploidy groups with a BS of 100% (Fig. 2 c). The diploid-type haplotype A was placed with haplotype B together. They differ only by one indel (Tab. 2). In the diploid

Tab. 2. Haplotypes of cpDNA in the Carpathians. Haplotype A – accessions nrs. 007, 017, 045, 049, 107; haplotype B – nrs. 026, 029, 50A, 057; haplotype C – nrs. 001, 009, 023, 025, 034, 047, 048, 066, 072 (see Tab. 1 and Fig. 1).

Haplotypes / nr. of site	Ploidy	117	250	322-328	367	545-551	552-555	607-614	635	656-662	794-801	821	871-880
Haplotype A		G	G	AAAAAAA	G	TTTTTT-	ATTT	TTTTTT-	G	-------	TTTTTT--	A	TTTTTTTTTT
Haplotype B		G	G	AAAAAAA	G	TTTTTT-	ATTT	TTTTTT-	G	-------	TTTTTTT-	A	TTTTTTTTTT
045 *A. d.* ssp. *degenii*		G	G	AAAAAAA	G	TTTTTT-	ATTT	TTTTTT-	G	-------	TTTTTTT-	A	TTTTTTTTTT
033 *A. l.* ssp. *lasiocarpum*	2n = 16	T	G	AAAAAA-	G	TTTTTT-	ATTT	TTTTTT-	G	-------	TTTTTTT-	A	TTTTTTTTTT
003 *A. v.* ssp. *variegatum*		G	G	AAAAAAA	G	TTTTTT-	ATTT	TTTTTT-	A	-------	TTTTTTT-	A	TTTTTTTTTT
065 *A.* ×*berdaui* (2n = 24)		G	G	AAAAAAA	A	TTTTTT-	ATTT	TTTTTT-	G	-------	TTTTTTT-	A	TTTTTTTTTT
059 *A. l.* ssp. *kotulae*		G	G	AAAAAAA	G	TTTTTT-	ATTT	TTTTTT-	G	-------	TTTTTT--	T	TTTTTTTTTT
Haplotype C		G	G	AAAAAAA	A	TTTTTTT	----	TTTTTTT	G	AATAATA	TTTTTTTT	T	TTTTTTTT--
054 *A. firmum* ssp. *fissurae*	2n = 32	G	A	AAAAAAC	A	TTTTTTT	----	TTTTTTT	G	AATAATA	TTTTTTTT	T	TTTTTTTT--
074 *A. bucovinense*		G	A	AAAAAAA	A	TTTTTTT	----	TTTTTTT	G	AATAATA	TTTTTTTT	T	TTTTTTTT--
032 *A.* ×*nanum*		G	G	AAAAAAA	G	TTTTTTT	----	TTTTTTT	G	AATAATA	TTTTTTTT	T	TTTTTTTT--

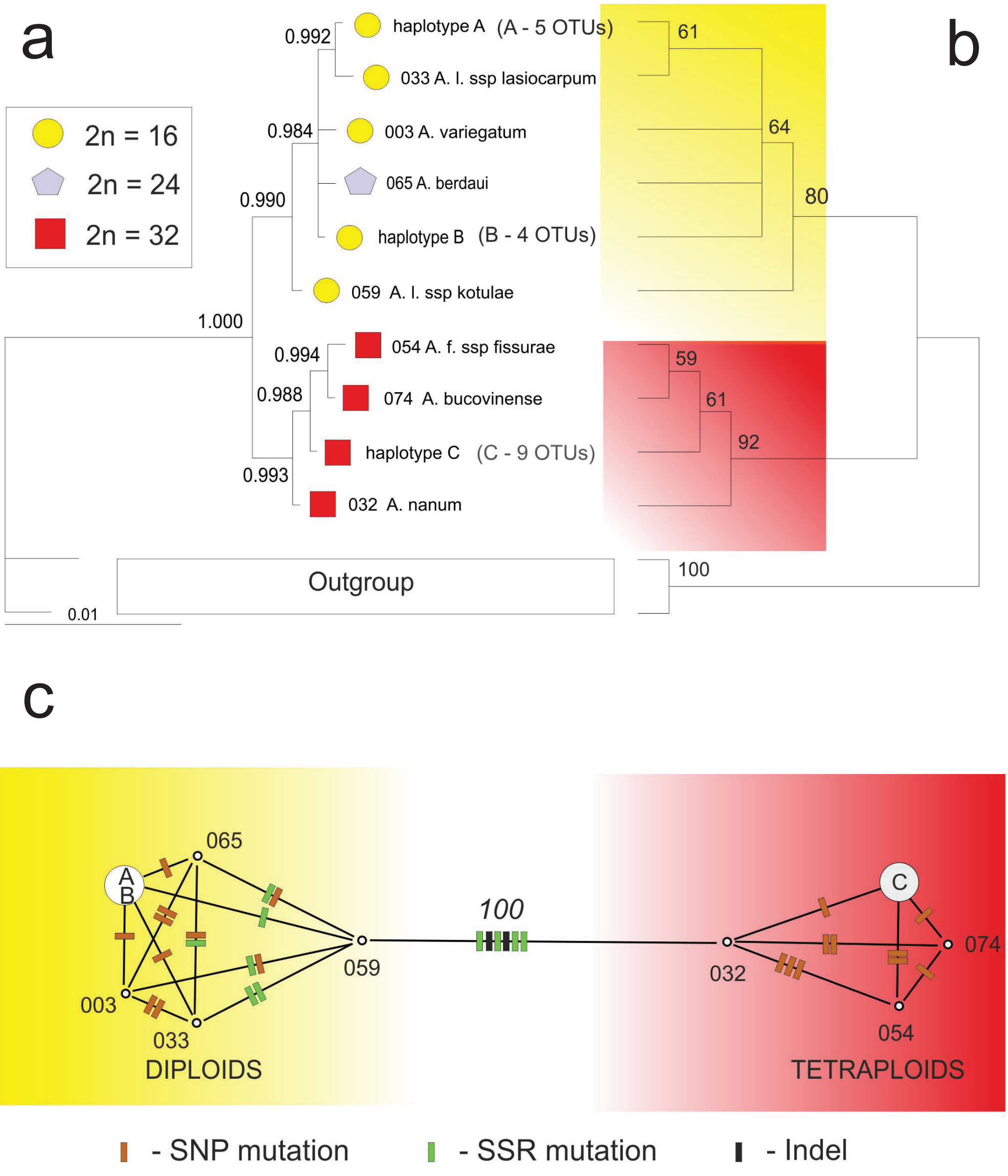

Fig. 2. a – Bayesian Inference (MrBayes) of cpDNA haplotypes of *Aconitum* subgen. *Aconitum* in the Carpathians (above nodes posterior probabilities are given); **b** – maximum parsimony analysis (PAUP*) and majority consensus tree (above nodes bootstrap values are given); **c** – minimum spanning network (SplitsTree). The split between the diploid-type and tetraploid-type cpDNA haplotypes is supported with 100% bootstrap. Bootstrap support for (b) and (c) is based on 1000 random runs. Haplotypes A, B and C are characterized in Tab. 2. **A. f.** – *Aconitum firmum*; **A. l.** – *Aconitum lasiocarpum*.

group both SSR and SNP mutations occurred and in the tetraploid group only SNP mutations were found.

Discussion

The studied chloroplast region in the subgen. *Aconitum* in the Carpathians is clearly different in the diploid *Cammarum* and tetraploid *Aconitum* groups. All the phylogenetic analyses showed the split between these cytogenetic/taxonomic groups. Three cpDNA haplotypes: A, B, and C were represented by more than one accession. cpDNA haplotypes A and B were characteristic of the diploids and cpDNA haplotype C of tetraploids. However, all three haplotypes were not the area or species specific. The remaining cpDNA haplotypes were singular and genetically very close to one the cpDNA haplotypes A, B and C, differing by up to two polymorphisms in diploids and up to three polymorphisms in tetraploids. The genetic affinity of *A. degenii* and *A. lasiocarpum* is weakly (51%) supported in MP.

Nucleotide variation of cpDNA is extremely low in the genus *Aconitum*. In the study on *Aconitum* subgen. *Lycoctonum* in Europe Utelli *et al.* (2000) found 1-2 point mutations in the *psb*A-*trn*H spacer. Similarly, some cpDNA sequences were identical and formed species-specific cpDNA haplotypes. Their specificity could be a result of the geographic isolation of the species. Authors claimed that minute differences in sequence data of the ITS and *psb*A-*trn*H intergenic spacers between *A. lycoctonum* (Alps, Carpathians, Pyrenees, Sierra Nevada), *A. moldavicum* (Carpathians), *A. septentrionale* (Northern Europe), and *A. orientale* (Cacucasus) put in question their taxonomic status as a separate species. According to our results the same cpDNA haplotype occurs in various species within the same ploidy level and rarely, in the effect of hybridization, among the ploidy levels. In this line of reasoning the taxonomical sections (diploids *vs.* tetraploids) in the Carpathians should gain a status of the singular species. In order to maintain a rational taxonomic *status quo* a solution is the morpho-geographical species concept. It attains a logical basis when the pattern of the morphological variability can be arranged in a geographical pattern (Cain 1974). The distribution of the same cpDNA haplotype in various species could be the result of the interspecific hybridization.

Our results show that cpDNA markers discriminated *Aconitum* at the sectional/ploidy level. Probably none of the diploids in the Carpathians was ancestral to any tetraploid species from the region. So, both sections could represent here various migratory and historical elements. A wider sampling, including the Asian representatives, could enlighten the problem. The tetraploid group of *Aconitum* in Europe belongs to the oligothermic, high-mountain flora. It represents currently the group of Arctic-Alpine plants (Hultén 1937) covering the boreal and arctic portions of northern hemisphere and the mountains of Europe and Asia. In the Carpathians this group (alongside with *Aconitum* sect. *Aconitum*) includes for example: *Athyrium distentifolium, Cerastium alpinum, Dryas octopetala, Hieracium alpinum, Juncus triglumis, Lloydia serotina, Oxyria digina*, and other (Zając & Zając 2009).

In studies on Asian *Aconitum* with the use of cpDNA and RFLP markers the two main clades were found, one of the eastern Asian diploids and the other of the so called Japenese tetraploid complex (Kita *et al.* 1995). The authors put forward a hypothesis that the entire complex had originated from one of the tetraploid species which populations, more or less isolated, adopted to alpine environmental conditions. It was because the authors were not able to find any genetic affinities of the tetraploid group to any diploid species studied. In another, supplementary studies Kita & Ito (2000) found that the missing link was a diploid *A. volubile* Koelle growing in Russia (the Ural Mts., E and W Siberia), Mongolia, China, Korea and Japan (see Mitka 2003). It suggests that this taxon could be ancestral to the tetraploids.

Similarly, if Carpathian diploids were ancestral to the tetraploids they should form a monophyletic group. It was not a case suggesting their different origins. One of the explanations could be that the diploids formed the oldest element, and their genetic roots could have been placed in pre-Pleistocene taking their different ecological profile as forest species. They could be linked genetically with temperate Central-Eastern Asian geoflora which might reach Europe as early as in the Early Oligocene. This is also traced in the similarities between European and Asian fossil floras of that period (Tiffney 1985; Mai 1995). Another hypothesis claims that the Arctic-Alpine flora originated in the late Tertiary in Eastern Siberia and Central Asia (Hultén 1937). Current studies corroborate this scenario, as for example phylogeography of *Ranunculus pygmeus* (Schönswetter *et al.* 2006), *Dryas octopetala* (Skrede *et al.* 2006), and *Saxifraga oppositifolia* (Winkler *et al.* 2012). Unexpectedly, the phylogeographic analysis revealed that the latter species has two ancestral areas: in Europe (the Alps) and in Central Asia. This infers that most likely there were other Early Tertiary genetic lineages in the Northern Hemisphere, in addition to the Central Asian. If this was the case, Central Asian Arctic-Alpine flora could not be regarded as the "cradle" but rather "museum". The other explanation is that both the diploids and tetraploids in the Carpathians represent the remnants of an old genetic European line and in fact both they are of the ancient, the pre-Pleistocene age (the result similar to *S. oppositifolia* mentioned above). It is a postulate of the complementary to the Central Asian genetic center of *Aconitum* in Europe. The third possibility is that the Carpathian (in wider context – the European) *Aconitum* had roots in the Asian genetic centre and the common descendant lineage extinct.

The present results showed that the tetraploid *A. bucovinense* was placed within both the diploid (haplotype B) and tetraploid groups. In fact, the species is considered as an old hybrid between *A. degenii* and *A. firmum* (Mitka 2003). On the other hand, it could be the effect of the recent transfer of the plastid gene. It has been often noted incongruence between the morphological-cytogenetic classification, nrDNA inferred phylogeny *vs.* chloroplast-based phylogeny that could be a sign of chloroplast capture (Rieseberg & Soltis 1991). The examples are *Aconitum* (Kita *et al.* 1995; Utelli *et al.* 2000), *Anthoxanthum* (Pimentel *et al.* 2013), *Hedyosmum* (Zhang *et al.* 2015), *Heuchera* (Soltis & Kuzoff 1995), *Meehania* (Deng *et al.* 2015), and *Paeonia* (Sang *et al.* 1997). The occurrence of the diploid-type cpDNA in the tetraploid species could be the effect of its hybridization with a diploid line.

The triploid species *A.* ×*berdaui*, a hybrid between the tetraploid *A. firmum* and diploid A. *variegatum*, was placed in the cpDNA diploid-type group. This hybrid was studied by Zieliński (1982a, 1982b) in the Tatra Mts. The author found the introgression of DNA loci of the nuclear genome from a diploid into a tetraploid line. This mechanism of introgression, from the diploid into the tetraploid species is also known as a triploid bridge (Husband 2004).

In conclusion, the two different types of haplotypes of cpDNA in the diploids and tetraploids in the Carpathians advocates for their independent origin in the mountain area. Probably this pattern of cpDNA diversity is typical for the whole Europe, a hypothesis to be checked based on a wider sampling. It makes *Aconitum* a promising object of the studies on the hybridization between the section *Aconitum* and section *Cammarum*.

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ATTEMPT OF A MORPHOLOGICAL DIFFERENTIATION OF *HELLEBORUS* SPECIES IN THE NORTHWESTERN BALKANS

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Abstract. The genus *Helleborus* is represented in the Northwestern Balkans by 8 species. Some of them (*H. atrorubens, H. foetidus* (newcomer, introduced as well as escaped from culture), *H. niger,* and *H. orientalis* (newcomer, escaped from culture)) are rather easy for determination and discrimination. While other 4 species (*H. dumetorum, H. multifidus, H. odorus,* and *H. viridis*) are really difficult for determination because of their narrow morphological similarity, which also is realized a wide variety in leaf shape. The distribution areas of last 4 species overlap in the Northwestern Balkans, so that there are no really clear borders of their distribution. Dominating species in this region is *H. multifidus,* and especially common there is its subsp. *istriacus*. Other 3 species are rare and are therefore often overlooked and the herbarium specimens are frequently misidentified as *H. multifidus*. Moreover, all these 4 species produce number of hybrids, and as a result all kind of transistions between these taxa could be found. In particular, 11 hybrides could be confirmed for this region. The hybrid between *H. dumetorum* and *H. multifidus* is described here as *Helleborus* ×*mucheri*.

Key words: *Helleborus*, Balkans, differentiation, distribution, hybrids, morphology, species, taxa

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Introduction

The Northwestern Balkans is a rather interesting region for *Helleborus* studies, because several species with overlapping areas are represented there (Starmühler 2007). The number of morphological characters is high enough for a good separation of all *Helleborus* species in the Northwestern Balkans. However, the problem is that in several cases you should use the leaf features in combination with the flower characteristics for a definite result. Besides the cultivation of plants collected in the field to see both, leaves and flowers, we have no other possibilities for absolutely correct determinations. Sometimes it is also possible to visit a habitat in nature in two different periods to see the growth and developing of these plants. But for the revision of herbarium material there is often no other way than to determine the specimen with the suffix *cf.*

Not only high variability of the most *Helleborus* species leds to descriptions of local taxa (Schiffner 1890). The problem is also increased by high number of hybrids, especially between the species in the section *Helleborastrum* (Bavcon *et al.* 2012). The situation becomes even more complicated with the anthropogenic introduction of alien species and their consequent escape from gardens (Pospichal 1898).

The highest variability we find in the shape of the basal leaves (Becker 2011), especially in *H. multifidus* subsp. *istriacus*, the most widespread and most frequent taxon in the Northwestern Balkans. For many years the closely related taxa (*H. dumetorum, H. multifidus, H. odorus,* and *H. viridis*) have not been separated or only partly separated in the literature dealing with this territory. In many cases all 4 species were lumped in a single taxon which was sometimes identified as *H. dumetorum* or *H. odorus,* and very often – as *H. viridis*. The first attempt to show the different areas of distribution of these species on maps was done 9 years ago (Starmühler 2007), while the attempt to find the morphological differences between all accepted taxa in this region was realized just in 2014 (Rottensteiner 2014) what also was reflected in the determination key.

Systematics

Helleborus Linnaeus 1753, Sp. Pl.: 557
  sect. ***Griphopus*** Spach 1839, Hist. Nat. Veget. Phan. 7: 319
    H. foetidus Linnaeus 1753, Sp. Pl.: 558
  sect. ***Helleborastrum*** (Spach) K. Werner & F. Ebel 1994, Flora 189: 98
    H. atrorubens Waldstein & Kitaibel 1812, Descr. et Icon. Pl. Rar. Hung. 2: 301, tab. 271
    H. dumetorum Waldstein & Kitaibel ex Willdenow 1809, Enum. Pl. 1: 592
      subsp. ***illyricus*** Starmühler 2007, Carinthia II 197/117: 413
    H. multifidus Visiani 1829, Flora (Regensburg) 12, Ergänzungsbl. 1: 13
      subsp. ***multifidus***
      subsp. ***istriacus*** (Schiffner) Merxmüller & Podlech 1961, Feddes Repert. Spec. Nov. Regni Veg. 64: 5
    H. odorus Waldstein & Kitaibel ex Willdenow 1809, Enum. Pl. Hort. Berol.: 592
      subsp. ***odorus***
      subsp. ***laxus*** (Host) Merxmüller & Podlech 1961, Feddes Repert. 64: 5
    H. orientalis Lamarck 1789, Encycl. 3: 96
    H. viridis Linnaeus 1753, Sp. Pl.: 558
      subsp. ***viridis***
  sect. ***Helleborus***
    H. niger Linnaeus 1753, Sp. Pl.: 558
      subsp. ***niger***
      subsp. ***macranthus*** (Freyn) Schiffner 1890, Bot. Jahrb. Syst. 11: 105

Descriptions

Helleborus atrorubens Waldstein & Kitaibel 1812, Descr. et Icon. Pl. Rar. Hung. 2: 301, tab. 271 (Fig. 1).

Plant 20-40 cm tall; stem without cauline leaves; leaves semi-coriaceus, not hardy, young ones ± hairy along the veins, later nude, dark green, divided into 7-11 leaflets; leaflets 2-7 cm broad, undivided, with nude veins; main veins not exserted, lateral veins not exserted; inflorescence with 1-9 flowers; bracts divided; flowers 4-5.5 cm broad, slightly drooping; tepals narrow-ovate to ovate, deep brown purple outside, pale purple inside; carpels 3-5, 15-18 mm long (without beak).

Ecology: Light woods and forest edges, meadows, vineyards, in dryer habitats than *H. dumetorum* and *H. odorus*.

Distribution: Southern Slovenia, Croatia, Bosnia, Serbia (see Bavcon *et al.* 2012).

Specimina selecta: Flora stiriaca exsiccata 168, Stiria inferior, in dumetis ad pagum Videm prope urbem Gurkfeld, solo calcareo, 180 m s.m.; 03.1905; leg. A.v. Hayek (GJO-59249).

Helleborus dumetorum Waldstein & Kitaibel ex Willdenow subsp. ***illyricus*** Starmühler 2007, *Carinthia* II 197/117: 413 (Figs. 2 & 3).

Plant 20-30 (-40) cm tall; stem without cauline leaves; leaves not hardy, divided into 7-11 (-13) leaflets, the central 3 ones always undivided, 1-3 cm broad, green to dark green, with hairy main veins; main veins little exserted, lateral veins not exserted; inflorescence with (2-) 3-5 (-6) flowers; bracts divided; flowers 3-4 (-5) cm broad, ± drooping; tepals narrow-ovate, pale green, cup-shaped, 2.5-3.5 (-4) cm broad; carpels 3-5; ripe fruit 15-18 mm long (without beak).

Ecology: Karst heath, light woods, shibliak, mostly on moist soil.

Distribution: Southwestern Slovenia, Friuli Venezia-Guilia, Northwestern Istria (the area of subsp. *dumetorum* ranges over Southern Austria, Slovenia, Eastern Croatia, Western Hungary, as well as Southwestern, Southern and Eastern Romania).

Specimina selecta: Istr.; leg. C. Albori (GZU).– Ex herbario florae illyricae, bey Triest häufig; s.d.; leg. M. Tommasini (GJO-1986/3665). – Zwischen Gebüsch auf … bey Triest; s.d.; leg. M. Tommasini (GJO-1856/3667). – Triest; s.d.; leg. Marchesetti (GJO-1915/876). – Triest; 03.; leg. Tommasini (GJO-1911/3878). – Flora exsiccata Austro-Hungarica 2541, Istria, in dumetis inter pagos Padric et Orleg; s.d.; leg. Solla (GZU). – Lippizer Wald; 03.1833; leg. … (GJO-1851/35). – Küstenland, Opcina; 04.1875; leg. Mitterdorfer (GZU). – Triest, Boschetto; 21.3.1880; leg. Penecke (GZU). – Flora von Triest, Karstwiesen bei Cattinara; 24.03.1889; leg. V. Engelhardt (GJO-1918/13341). – Triest; 02.1893; leg. Raumhart (GJO-1908/4546). – Auf Karstwiesen

Fig. 1. Young inflorescence of *Helleborus atrorubens.*

bei Triest; 04.1901; leg. J. Müller (GZU). – Istrien, lichte Wälder bei Draga; 03. –06.1908; Herb. I. Dörfler (GZU). – J, Istrien, Ucka; im Laubwald, unter Gebüsch; 22.05.1969; leg. Schiefermair (GJO-25343). – Italien, Triestino/Territorium von Triest, E Trieste/Triest, etwa 0,2 km NW Trebiciano/Trebče/Trebich, N 45°40,57', E 13°49,16', 340 m alt.; *Pinus nigra*-Wald; 17.03.2001; leg. W. Starmühler (GJO, GZU, IBF, KL, LJU, TSB, W, WHB), Typen. – Italien, Triestino/Territorium von Triest, E Trieste/Triest, 0,15 km SE Padriciano/Padriče/Padrich, N 45°38,99', E 13°50,40', 365 m alt.; *Pinus nigra*-Wald; 17.03.2001; leg. W. Starmühler (GZU, KL, LI, WU, Herb. D. Koriakov/RU-Novosibirsk). – Italien, Triestino Territorium von Triest, E Trieste/Triest, 0,5 km NE Basovizza/Bazovica/Basowitz, N 45°38,81', E 13°52,42', 380 m alt.; Trockenrasen; 17.03.2001; leg. W. Starmühler (KL). – Slowenien, Triestino/Territorium von Triest, E Trieste/Triest, an der Straße von Basovizza/Bazovica/Basowitz nach Lokev/Corgnale, an der Abzweigung der Straße nach Lipica/Lippiza/Lipizza, N 45°39,58', E 13°53,43', 410 m alt.; *Pinus-Quercus*-Wald; 17.03.2001; leg. W. Starmühler (KL). – Slowenien, Istrien, Čičarija/Cicceria, S Kozina/Cosina, am Weg von Podgorje/Piedimonte del Taiano auf den Berg Slavnik/M. Taiano/Slaunig, N 45°31,185', E 13°58,179', 749 m alt.; Karstheide; 14.05.2010; leg. V. Mikoláš, W. Mucher & W. Starmühler (KL).

Helleborus foetidus Linnaeus 1753, Sp. Pl.: 558 (Fig. 4).

Plant 20-80 cm tall; stem branched, with several cauline leaves; leaves divided into 3-9 leaflets; leaflets narrow lanceolate; inflorescence with usually more than 10 flowers; bracts undivided, ovate; flowers 1-2.5 (-3) cm broad, bell-shaped, ± drooping; tepals green with dark red margins; carpels 3 (-4).

Ecology: Light woods, forest edges and shibljak on little dry to moist soil.

Distribution: Western and Southern Europe from South England to Northern Africa (this species is a newcomer in the Northwestern Balkans. It has been anthropogenicly introduced and escaped from culture as well (Pospichal 1898)).

Specimina selecta: Tüffer, Stmk; s.d.; s.n. (GJO). – Bei Tüffer Cill. Dr.; s.d.; leg. Profenc (GJO).

Helleborus multifidus Visiani 1829, Flora (Regensburg) 12, Ergänzungsbl. 1: 13 (Figs. 5-7).

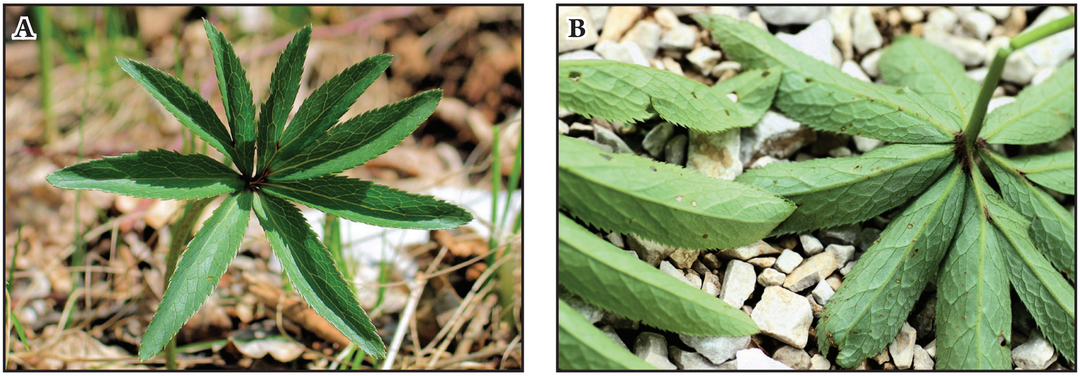

Fig. 2. *Helleborus dumetorum* subsp. *illyricus*: **A** – lamina of a basal leaf; **B** – underside of a basal leaf with a litte excerting main vein and not exserting lateral veins.

Fig. 3. Flower of *Helleborus dumetorum* subsp. *illyricus* with narrow ovate tepals.

Plant 25-45 cm tall; stem mostly without cauline leaves; leaves not hardy, divided into 11-50 leaflets; inflorescence with 3-8 flowers, arranged vertically; bracts divided; flowers 3.5-5.5 cm broad, cup-shaped; tepals broad-lanceolate to narrow-ovate, yellowish or pale green; carpels 3-6; ripe fruit 18-20 mm long (without beak).

Ecology: Shrubbery edges, light woods, shibliak, often in dry habitats, more than all other species in this region.

Distribution: Southernmost Switzerland (Tessin), Northeastern Italy, Southwestern Slovenia, Croatia, Bosnia-Herzegovia, Montenegro.

Fig. 4. Habitus of *Helleborus foetidus.*

subsp. ***istriacus*** (Schiffner) Merxmüller & Podlech 1961, Feddes Repert. Spec. Nov. Regni Veg. 64: 5 (Figs. 5 & 6).

Leaflets more than 2 cm broad, some of them divided almost to the base, some only to the middle, at the margin more finely toothed.

Distribution: Southernmost Switzerland (Tessin), Northeastern Italy, Southwestern Slovenia, Croatia, Bosnia.

Specimina selecta: Flora von Istrien, Monte Maggiore; 05.1873; leg. Rossi (GZU). – Sehr gemein auf den Vorbergen des Monte Maggiore bei Abbazia; 20.05.1887; Herb. K. Fritsch (GZU). – Istrien, Cherso; 03.06.1896; leg. K. Wilhelm (WHB). – Abbazia, Istrien; 04.1897; leg. Kuchler (GJO-1918/13334). – Flora Istriaca, Abbazia; 04./05.[18]97; leg. A. Steffeck (WHB). – Abbazia; 04.04.1897; leg. L. Richter (GZU). – Istrien, Monte Maggiore bei Fiume, 1396 m; 03.05.1897; leg. I. Ostermaier (GZU), 2 Belege. – Istria, in dumetis et in apricis collib. lapidosis totius littorio liburnici, Monte Maggiore; 30.04.1898; leg. Evers (GZU). – Istrien, auf Bergwiesen des Monte Maggiore, ca. 1000 m; 05.1900; leg. F. Vierhapper (WHB). – Istrien, an schattigen Stellen des Monte Maggiore bei Veprinaz, ca 800 m; 05.1900; leg. F. Vierhapper (WHB), 2 Belege. – Italien, Istrien, Carre bei Albona d´Istria; 03.1926; leg. R. Czagka jun. (GZU). – Istrien, Kraj; Karstbusch; 13.03.1957; leg. A. Neumann (KL-131506). – Mitteleuropäisches Gebiet, Provinz der Alpenländer, Karst und Karniolisch-illyrisches Übergangsgebiet, Karstwiesen zwischen Divača und Senožeče; 05.06.1958; leg. E. Habeler (GJO-26481/732). – Karst und Karniolisch-illyrisches Übergangsgebiet, Karstwiesen zw. Divača und Senožeče; 05.06.1958; leg. F. Wolkinger (GJO-26825/472). – Borgo Grotta Gigante (TS); 04.04.1966; leg. L. Poldini (TSB-028285). – Opicina; 02.04.1967; leg. S. Pignatti (TSB-028310). – Banne (TS); 12.04.[19]67; leg. Mortin (TSB-028427, TSB-028428, TSB-028430). – Flora v. Jugoslawien, Kroatien, Istrien, Učka Gora bei Opatija, Fagetum b. Hotel Učka; 01.07.1967; leg. Leute & Tomšovic (KL-115421). – Monte Orsaro pr. Fernetti; 11.04.1968; leg. S. Pignatti (TSB-028417, TSB-028418, TSB-028419, TSB-028420, TSB-028421). – Fr. la chiesa di Truski (Capodistria); 17.04.1971; leg. S. Pignatti (TSB-028294, TSB-028295). – Učka, 950 [m], Yu.; 06. [19]71; leg. W. Holzner (WHB). – Jugoslawien, Istrien, SW von Plomin, ca. 54 km NE von Pula; 02.11.1973; leg. W. Möschl & H. Pittoni (GZU). – Croatia, Istria, in silvis - *Carpinetum orientalis* - supra sinum maris Limski kanal dictum, solo calcareo, 20 m s.m., 0848/3; 17.03.1974; leg. E. Mayer & T. Wraber (GJO-26.245/56, GZU, LJU). – Monte Cocusso, m. 500; 11.04.[19]75; leg. C. Longhi (TSB-028237). – Istrien, Ucka = Mte. Maggiore im NE der HI Istrien, lichter *Fagus s.* + *Pinus nigra*-Wald, ca. 1120 m;

Fig. 5. Basal leaf of *Helleborus multifidus* subsp. *istriacus*.

03.05.1975; leg. W. Möschl & H. Pittoni (GZU). – Flora Italiae, prov. di Trieste, tra Opicina e M.te Orsario, 300 m s.m.; 03.05.1975; leg. E. Cristancig (TSB-028236). – Flora v. Jugoslawien, Kroatien, Istrien, am Aufstieg vom Poklon-Sattel zur Učka Gora SW Opatija, Laubmischwald, Kalk, 950 m; 28.05.1977; leg. G.H. Leute (KL-115420). – Flora von Kroatien, in einem sommergrünen Eichenwald auf der Insel Cres; 25.04.1980; leg. W. Forstner (WHB). – Istrien, Tinjan b. Pazin, Nr. 007558; 22.08.1982; leg. A. Kofler (IBF). – Flora von Jugoslawien, Slowenien, Istrien, Karstwiese Sw Črnotiće oberh. Črni Kal, Kalk; 18.05.1991; leg. G.H. Leute (KL-115419). – Slowenien, Istrien (Istria, Istra), Golf von Triest (Golfo di Trieste, Tržaški zaliv), SE Triest (Trieste), am Weg von Ospo (Osp) nach Castelz (Kastelec), W-Hang des M. Carso (Kras), N 45°34,43’, E 13°51,62’, 165 m alt.; *Acer monspessulanum-Fraxinus ornus-Quercus pubescens*-Wald mit *Ostrya carpinifolia*; 05.07.1997; leg. W. Starmühler (KL). – Italien, Territorium von Triest (Triestino), E Triest (Trieste), 0,5 km ENE Basovizza, N 45°38,81’, E 13°52,40’, 360 m alt.; Gebüschsaum; 06.07.1997; leg. W. Starmühler (KL). – Slowenien, Territorium von Triest (Triestino), E Triest (Trieste), 1 km S Lipizza (Lipica), N 45°39,52’, E 13°52,42’, 385 m alt.; Gebüschsaum; leg. W. Starmühler (GJO, KL, LG). – Kroatien, Istrien (Istria, Istra), Tschitschenboden (Cicceria, Ćićarija), NE Pinguente (Buzet), S-Hang des M. Sbevnizza (Žbevnica), N 45°27,30’, E 14°01,69’, 845-950 m alt.; Pinus-Wald mit *Fraxinus ornus, Ostrya carpinifolia* und *Sorbus aria*; 26.07.1997; leg. W. Starmühler (KL). – Kroatien, Istrien (Istria, Istra), Gebiet des Monte Maggiore (Učka gora), N Fianona (Plomin), am Weg von der Kirche des Hl. Georg (S. Giorgio, Sv. Juraj), zur Ruine Wachsenstein (Kozljak), W Catun (Katun), N 45°10,93’, E 14°11,04’; 135 m alt.; Gebüschsaum; 21.05.1998; leg. H., U. & W. Starmühler (KL). – Kroatien, Istrien (Istria, Istra), Hinterland von St. Veit (Entroterra di Fiume), SW Clana (Klana), 2 km ESE Škalnica, N 45°26,41’, E 14°21,09’, 570 m alt.; Gebüschsaum; 03.06.1998; leg. W. Starmühler (KL). – Kroatien, Istrien (Istria, Istra), Tschitschenboden (Cicceria, Ćićarija), S Neuhaus (Castelnuovo, Podgrad), 1 km SW Klein-Mune (Mune Piccolo, Male Mune), N 45°27,18‘, E 14°08,78‘, 650 m alt.; Gebüschsaum; 24.04.1999; leg. U. & W. Starmühler (KL). – Kroatien, Istrien (Istria, Istra), West-Küste (Costa occidentale, Zapadna obala), am Weg vom Leme-Kanal (Canale di Leme, Limski zaljev) nach Due Castelli (Dvigrad), N 45°07,29’, E 13°45,92’, 25 m alt.; Gebüschsaum; 06.05.2000; leg. U. & W. Starmühler (GZU, KL). – Italien, Triestino/Territorium von Triest, E Trieste/Triest, 0,5 km NE Basovizza/Bazovica/Basowitz, N 45°38,81’, E 13°52,42’, 380 m alt.; Trockenrasen; 17.03.2001; leg. W. Starmühler (GZU, KL). – Slowenien, Tržaško/Triestino/Territorium von Triest, E Trieste/Triest, Lipica/Lippiza/Lipizza, N 45°40,82’, E 13°53,32’, 410 m alt.; Gebüschsaum; 17.03.2001; leg. W. Starmühler

Fig. 6. Flower of *Helleborus multifidus* subsp. *istriacus* with ovate yellowish green tepals.

(GZU, KL, LJU). – Slowenien, Istrien, Brkini/Berchinia/Berkin, ESE Kozina/Cosina, 0,3 km NNE Tublje/Tubliano, N 45°35,90', E 13°58,43', 535 m alt.; Gebüschsaum; 17.03.2001; leg. W. Starmühler (GJO, GZU, KL, LJU und WHB). – Flora Croatiae, Krk (Veglia), lungo il sentiero che da Treskovac porta a Vrbnik; 13.04.[2]001; leg. L. Poldini (TSB-028399). – Flora von Kroatien, Istrien, lichter Wald bei Žejane; 06.07.2001; leg. K.-G. Bernhardt (WHB). – Kroatien, Istrien, Zaledje Rijeke/Entroterra di Fiume/Hinterland von St. Veit, etwa 3 km SSW Klana/Clana/Klan, an der Straße nach Studena, N 45°24,89', E 14°23,42', 520 m alt.; Gebüschsaum; 01.05.2001; leg. W. Starmühler (GJO, KL). – Slowenien, Istrien, Brkini/Berchinia/Berkin, ESE Podgrad/Castelnuovo d'Istria/Neuhaus, etwa 1 km NNE Starod/Starada, N 45°31,00', E 14°11,89', 755 m alt.; Waldrand; 03.05.2001; leg. W. Starmühler (KL). – Slowenien, Istrien, Notranja Istra/Istria interna/Inner-Istrien, E Koper/Capodistria/Gavers, zwischen Kortine/Sali und Kubed/Covedo, E-Hang der Krasca, N 45°31,75', E 13°52,80', 180 m alt.; Waldrand; 19.02.2002; leg. U. & W. Starmühler (KL). – Kroatien, Istrien, Zapadna obala/Costa occidentale/West-Küste, NE Rovinj/Rovigno/Rofein, N-Hang zum Limski kanal/Canale di Leme/Leme-Kanal S Lim/Leme, N 45°07,74', E 13°44,38', 5-10 m alt.; *Ostrya carpinifolia*-*Quercus pubescens*-Wald; 23.02.2002; leg. F., U., W. & W.A. Starmühler (GZU, KL). – Slowenien, Istrien, Brkini/Berchinia/Berkin, etwa 2 km WNW Podgrad/Castelnuovo d'Istria/Neuhaus, N 45°31,88', E 14°07,51', 550 m alt.; Karstheide; 29.05.2002; leg. U. & W. Starmühler (KL). – Flora von Kroatien, bei Zeijane; 22.04.[20]03; leg. K.-G. Bernhardt (WHB-44569, WHB-44570). – Flora von Kroatien, zw. Divici u. Sarici, N 44°57,668', E 14°00,425'; 24.04.[20]03; leg. K.-G. Bernhardt (WHB-44567). – Flora von Kroatien, bei Novigrad; 24.04.[20]03; leg. K.-G. Bernhardt (WHB-44568). – Kroatien, Istrien, Insel Cres/Cherso, NNW Cres/Cherso, Bucht Sv. Blaž/S. Biaggio W von den Ruinen des Klosters Sv. Blaž/Hl. Blasius, N 45°00,40', E 14°21,04', 5 m alt.; *Olea europaea*-Gebüsch; 01.05.2003; leg. U. & W. Starmühler (GZU, KL, ZA). – Italien, Triestino/Territorium von Triest, NE Trieste/Triest, NNE Villa Opicina/Opčine/Optschina, bei der Foiba Opicina, N 45°41,87', E 13°48,17', 305 m alt.; lichter *Fraxinus ornus*-Wald; 17.05.2004; leg. W. Starmühler (GJO, GZU, KL). – Kroatien, Istrien, Ćićarija/Cicceria/Tschitschenboden, Kastavska šuma/Bosco di Castua/Khöstauer Wald NW Rijeka/Fiume/St. Veit am Pflaumb, Mali Brgud/Bergut piccolo/Klein-Bergud, 340 m alt.; Trockenrasen, Kalk; 28.05.2005; leg. W. Neuner & P. Vergörer (KL). – Kroatien, Istrien, Riječki zaljev/Golfo di Fiume/Golf von St. Veit: SE Labin/Albona, am Weg von Rabac/Porto Albona zur Siedlung Vlachi, E-Hang des M. Gherzi, N 45°03,915', E 14°08,465', 165 m alt.; *Quercus ilex*-Waldrand; 14.04.2006; leg. W. Mucher sen. & W. Starmühler (GZU, KL, ZA, Herb. D.Koriakov/RU-Novosibirsk). – Kroatien,

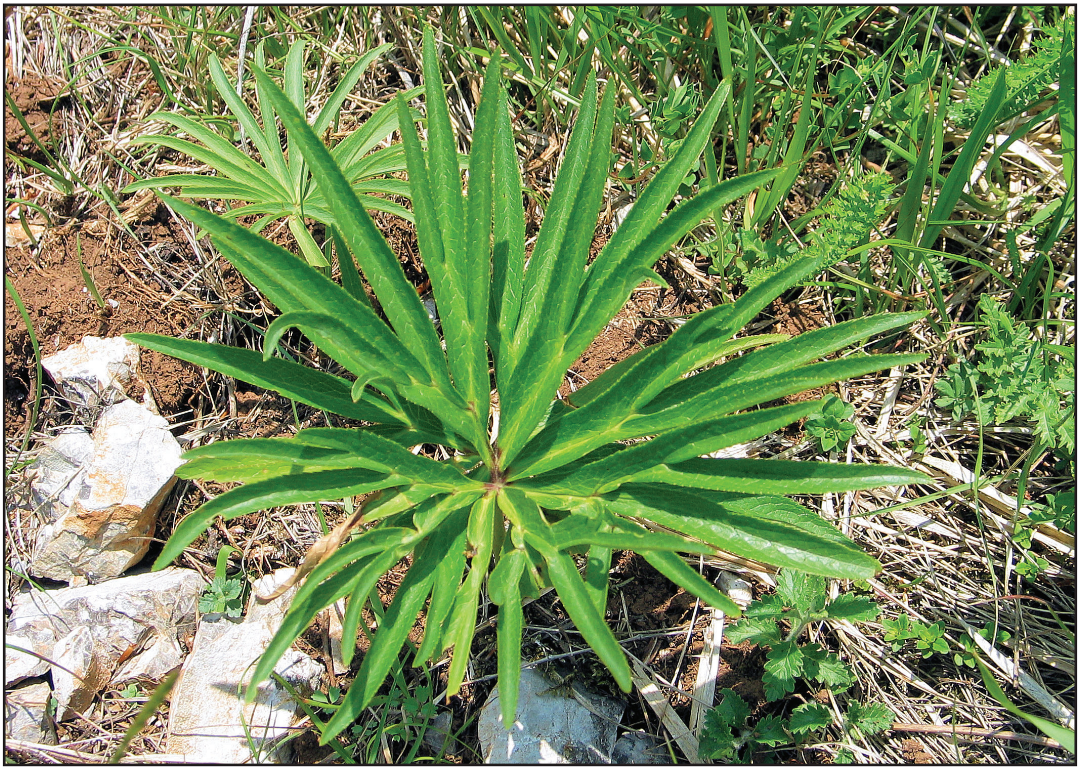

Fig. 7. Basal leaf of *Helleborus mutifidus* subsp. *multifidus*.

Istrien, Zaledje Rijeke/Entroterra di Fiume/Hinterland von St. Veit, 0,2 km S Rupa/Ruppa, N 45°28,153’, E 14°17,225’, 450 m alt.; Karstheide; 18.02.2007; leg. U. & W. Starmühler (GZU, KL, ZA). – Kroatien, Istrien, Učka gora/Territorio del Monte Maggiore/Gebiet des Monte Maggiore, NNE Labin/Albona, am Weg von Plomin/Fianona auf den Berg Kalić, N 45°08,673’, E 14°10,660’, 255 m alt.; Schibliaksaum; 19.02.2007; leg. U. & W. Starmühler (KL). – Kroatien, Istrien, Ćićarija/Cicceria/Tschitschenboden, SW Opatija/Abbazia, an der Straße von Veprinac/Apriano/Waprinitz auf den Poklon-Sattel, W-Hang des Berges Crkveni vrh/M. Chiesa, N 45°19,201’, E 14°14,148’, 744 m alt.; Gebüschsaum; 21.02.2007; leg. W. Starmühler (GJO, GZU, IBF, JACA, KL, W, WHB, ZA). – Flora von Kroatien, Istrien, Kvarner Inseln, Krk, Glavotok, Straße zum Campingplatz, „Urwald“, N 45°05’29”, E 14°26’16”, 28 m NN; 09.05.2008; leg. K.-G. Bernhardt (WHB-47824). – Kroatien, Istrien, Insel Cres, Straße von Porozina nach Cres N der Abzweigung nach Beli, N vom Krzic-Sattel, großflächige Salbei-Bestände, 450 msm, 45°03’48” N, 14°21’37” E ± 10”; 21.05.2009; leg. P. Pilsl (Herb. P. Pilsl-20288/A-Salzburg). – Slowenien, Istrien, Čičarija/Cicceria, S Kozina/Cosina, am Weg von Podgorje/Piedimonte del Taiano auf den Berg Slavnik/M. Taiano/Slaunig, N 45°31,185’, E 13°58,179’, 749 m alt.; Karstheide; 14.05.2010; leg. V. Mikoláš, W. Mucher & W. Starmühler (KL). – Slowenien, Istrien, SE Koper, Kraški rob, SE Zazid, am Beginn der großen Wiesenfläche, Saum, Alt: 631 m, E 13°57’15”, N 45°29’14”; 04.06.2010; leg. M.M. & K. Wernisch (WHB-051214). – Kroatien, Istrien, Zapadna obala/Costa occidentale/West-Küste, ENE Poreč/Parenzo, bei Antonci/Pribetici/Antonzi, 80 m alt.; Schibliaksaum, Terra rossa; 18.05.2011; leg. P. Vergörer (KL). – Kroatien, Istrien, Quarner Bucht, otok Krk/isola Veglia/Insel Vögls, Ostküste, NNW Vrbnik/Verbenico, am Weg von der Uvala Melska nach Risika, N 45°05,925’, E 14°39,587’, 53 m alt.; Macchiensaum; 24.03.2012; leg. W. Mucher sen. & W. Starmühler (GJO, GZU, KL, M, MBM, WU, ZA). – Slowenien, Istrien, von Zazid nach Brezec, Wanderweg oberhalb der Bahnlinie, Hopfenbuchen-Mischwald; 25.03.2012; leg. M.-L. Oschatz (WHB-056960). – Kroatien, Istrien, an Autobahnabfahrt Zimy, an Parkplatz, Niederwald, Alt: 394 m, E 13°53’17,6”, N 45°08’12,5”; 12.04.2012; leg. K.-G. Bernhardt & E. Naumer-Bernhardt (WHB-056541, WHB-056542). – Kroatien, Istrien, NW Klostar, Weg zum Palud-Puc-“See”, Niederwald, Alt: 88 m, E 13°41’13,0”, N 45°08’51,8”; 13.04.2012; leg. K.-G. Bernhardt & E. Naumer-Bernhardt (WHB-056543).

subsp. ***multifidus*** (Fig. 7).
Leaflets less than 2 cm broad, mostly divided

Fig. 8. *Helleborus niger* subsp. *niger*.

almost to the base, at the margin only distant and coarsely toothed.

Distribution: Croatia, Bosnia and Herzegovina, Montenegro (this subspecies occurs mainly in the southern part of this area, in the Northwestern Balkans there are no more larger populations, often only some few plants and often transitions to the subsp. *istriacus*).

Specimina selecta: Istrien, Slavnik b. Triest, buschige Orte; 05.1911; leg. Arbesser (GZU). – Jugoslawien, Bosnien, Dinarisches Gebirge, Osječenica, Umgebung von Kolunic SSW Bosanski Petrovac; Schafweide am Rande eines Buchen-Fichten-Tannenwaldes; 10.09.1988; leg. D. Ernet (GJO-25.844/47). – Kroatien, Istrien (Istria, Istra), Tschitschenboden (Cicceria, Ćićarija), Veprinazer Wald W St. Veit am Pflaumb (Fiume, Rijeka), S-Hang des M. Makljen, N 45°19,56', E 14°12,77', 1085 m alt.; Gebüschsaum; 02.06.2000; leg. P. Hofman, B. Mestel & W. Starmühler (GZU, KL).

Helleborus niger Linnaeus 1753, Sp. Pl.: 558 (Fig. 8).

Plant 13-20 (-30) cm tall; stem without or rarely with 1 or 2 cauline leaves, mostly not branched; leaves coriaceous, dark green on the upper side, green below, hardy, divided into 7-9 leaflets; inflorescence with 1-2 flowers; bracts undivided, not serrate; flowers 1-2 (-3), 5-9 (-11) cm broad; tepals broad-ovate, white; carpels mostly 7; ripe fruit about 3 cm long.

Ecology: Light woods, forest edges, on humous soil.

Distribution: Central and Eastern Alps, in the south to the Apennines, in the east to the Carpathians.

subsp. ***macranthus*** (Freyn) Schiffner 1890, Bot. Jahrb. Syst. 11: 105.

Leaflets lanceolate, broadest in the central part; the margin toothed or spiky toothed; flowers 7-9 (-11) cm broad; tepals after anthesis mostly violet.

Distribution: From South-Tyrol to the Swiss Kanton Tessin. Not native in the Northwestern Balkans, but on some places anthropogenicly introduced (Lausi 1964).

Fig. 9. Basal leaf of *Helleborus odorus* subsp. *odorus*.

subsp. ***niger*** (Fig. 8).

Leaflets broad lanceolate to obovate, rhomic, broadest in the terminal part, the margin toothed at the apex; flowers 5-8 cm broad; tepals after anthesis greenish.

Distribution: Central and Eastern Alps, in the south to the Apennines, in the east to the Carpathians (in the Northwestern Balkans only in the northernmost part in Slovenia).

Specimina selecta: Wälder bei Lichtenwald, Tüfer, mit *H. atrorubens* u. *H. viridis*; s.d.; leg. Maly (GJO-59572). – Römerbad Tüffer, steir. Wälder; 06.; Herb. J.B. de Fürstenwärther (GJO-59571). – Jugoslawien, Savetal bei Zagorje; Kalk; 04.1977; Herb. W. Rössler (GJO-26236/73).

Helleborus odorus Waldstein & Kitaibel ex Willdenow 1809, Enum. Pl. Hort. Berol.: 592 (Fig. 9).

Plant 30-50 (-60) cm hoch; stem without cauline leaves; leaves hardy, divided into 5-11 leaflets; leaflets not divided, lanceolate to broad-lanceolate, 1.5-6 cm broad, with serrate margin, veins thick, glandular pilose; inflorescence with 2-4 flowers; flowers 5-7 cm broad; tepals almost circular, yellowish to yellowish green; carpels (4-) 5; ripe fruit 15-20 mm long (without beak).

Ecology: Schrubbery edges, shibliak, light woods.

Distribution: Northern Italy, Slovenia, Croatia, Bosnia and Herzegovina, Serbia, Southern Hungary, Southern Romania, Northern Bulgaria.

subsp. ***laxus*** (Host) Merxmüller & Podlech 1961, Feddes Repert. 64: 5.

Leaves divided into 5-7 leaflets; leaflets mostly incised to 2-5 segments.

Distribution: Only in the Northwestern Balkans in Slovenia and Northern Croatia.

Specimina selecta: Divacca a. Karst, in Massen; 05.1906; leg. A.V. Hayek (GJO). – Slowenien, Tržaško/Triestino/Territorium von Triest, E Trieste/Triest, Lipica/Lippiza/Lipizza, N 45°40,82', E 13°53,32', 410 m alt.; Gebüschsaum; 17.03.2001; leg. W. Starmühler (GZU, KL).

subsp. ***odorus*** (Fig. 9).

Leaves divided into 7-11 leaflets; leaflets not incised.

Distribution: Northern Italy, Slovenia, Croatia, Bosnia and Herzegovina, Serbia, Southern Hungary, Southern Romania, Northern Bulgaria.

Specimina selecta: Istria, Mattuglie; 11.02.1899; leg. Evers (GZU), 2 Belege. – Istria, in dumetis et in apricis collib. lapidosis totius littorio liburnici, Mattuglie; 11.02.1899; leg. Evers (GZU). – Truski a S di Capodistria, m. 350; 17.04.1971; leg. S. Pignatti (TSB-028289). – Fr. la chiesa di Truski (Capodistria); 17.04.1971; leg. S. Pignatti (TSB-028290, TSB-028291, TSB-028292, TSB-028293). – Italien, Territorium von Triest (Triestino), E Triest (Trieste), 0,5 km ENE Basovizza, N 45°38,81', E 13°52,40', 360 m alt.; Gebüschsaum; 06.07.1997; leg. W. Starmühler (KL). – Italien, Triestino/Territorium von Triest, E Trieste/Triest, etwa 0,2 km NW Trebiciano/Trebče/Trebich, N 45°40,57', E 13°49,16', 340 m alt.; *Pinus nigra*-Wald; 17.03.2001; leg. W. Starmühler (GJO, GZU, KL, WHB). – Italien, Triestino/Territorium von Triest, E Trieste/Triest, 0,15 km SE Padriciano/Padriče/Padrich, N 45°38,99', E 13°50,40', 365 m alt.; *Pinus nigra*-Wald; 17.03.2001; leg. W. Starmühler (GZU, IBF, KL, WU, Herb. D. Koriakov/RU-Novosibirsk). – Slowenien, Istrien, Notranja Istra/Istria interna/Inner-Istrien, S Koper/Capodistria/Gavers, Ivankovec N Raven/S. Pietro dell'Amata, N 45°28,23', E 13°40,28', 40 m alt.; Waldrand; 18.03.2001; leg. H. Mucher & W. Starmühler (GZU, KL). – Slowenien, Istrien, Čičarija/Cicceria/Tschitschenboden, S Kozina/Cosina, am Weg von Podgorje/Piedimonte del Taiano auf der Forststraße auf den Berg Slavnik/M. Taiano/Slaunig, N 45°31,192', E 13°57,952', 801 m alt.; Waldrand; 26.09.2010; leg. V. Mikoláš & W. Starmühler (GZU, KL, LJU).

Helleborus orientalis Lamarck 1789, Encycl. 3: 96.

Plant 20-60 cm tall; stem without leaves, branched; leaves coriaceous, dark green, hardy, divided into 7-11 leaflets; bracts 3- to 5-partite, serrate; flowers (1-) 3-7, 6-9 cm broad; tepals purple.

Ecology: Shibliak and light woods.

Distribution: From Turkey to the Caucasus (In the Northwestern Balkans this species is a newcomer escaped from culture.).

Specimina selecta: Flora Italiae, prov. TS, Opicina-dolina; 08.04.1964; leg. L. Poldini (TSB-028439, TSB-028440).

Helleborus viridis Linnaeus 1753, Sp. Pl.: 558 subsp. ***viridis*** (Fig. 10).

Plant 20-40 (-50) cm tall; stem without or with 1-2 cauline leaves with 3 (-5) leaflets; leaves not hardy, with 7-17 leaflets; leaflets narrow-lanceolate, 1-2 cm broad, with serrate margin, veins narrow, glandular pilose, dark green on the upper side, not so dark green on the underside; inflorescence with 1-3 (-4) flowers; flowers 4-5 cm broad; tepals broad-ovate, green; carpels 3-5; fruit 25-28 mm long (without beak).

Ecology: Shrubbery edges, shibliak, light woods, meadows.

Distribution: Western and Central Europe southeastwards to Northern Italy and Northern Istria.

Specimina selecta: Pflanzen aus dem Karst bei Triest; s.d.; leg. V. Stephanides (GZU). – Triest; s.d.; leg. Hillenbrand (GJO-1851/40). – Triest; 03.1877; leg. Mittendorfer (GZU). – Flora von Istrien, Triften bei Canfanaro; 20.02.1892; leg. K. Untchj (GZU). – Istria, Volosca, ad viam Flumens; 23.02.1894; leg. Evers (GZU), 2 Belege. – Istria, Abbazia; 02.-03.1898; leg. Evers (GZU). – Istria, in dumetis et in apricis collib. lapidosis totius littorio liburnici, Volosco; 23.02.1899; leg. Evers (GZU). – Nördlich Triest, Karstwiese; 02.04.1961; s.n. (GZU), 2 Belege. – Ucka, Wiese; 30.04.1973; leg. I. Thaler (GZU). – Kroatien, Rupa SSE Ilirska Bistrica, ca. 460 m; Gebüschränder, Karstrasen; 19.04.1989; leg. E. Bregant (GJO-25.880/51, GJO-25.880/52). – Jugoslawien, Kroatien, Istrien, zwischen Buzet und Dolenja Vas, Umgebung von Roč; Kalk, Karstwiesen; 12.04.1990; leg. R. Karl (Herb. R. Karl/Köflach).

Hybrids

Helleborus atrorubens* × *H. odorus

This hybrid differs from *H. atrorubens* by leaves with exserted veins, by larger, greenish purple flowers, by ovate tepals. From *H. odorus* it differs by smaller flowers with light purple tepals, which remain slightly drooping.

Helleborus atrorubens* × *H. viridis* = *Helleborus* ×*viridescens Schiffner 1896, Denkschr. Akad. Naturforsch. Ivi.: 176.

This hybrid can be distinguished from *H. atrorubens* by leaves with exserted veins, larger and greenish purple flowers, and broad ovate tepals. From *H. viridis* it differs by flowers with light purple tepals, which remain slightly drooping.

Fig. 10. *Helleborus viridis* with broad ovate green tepals.

Helleborus dumetorum × ***H. multifidus*** = ***Helleborus*** ×***mucheri*** Rottensteiner *nothospec. (hybr.) nov.* (Figs. 11-13).

Diagnosis: Notae hybridae inter parentes erunt, imprimis nerva, pubescentia, forma sectioque foliorum, forma et magnitudo tepalorum.

From *H. dumetorum* it differs by hairy leaves with more leaflets and with exserted veins, and from *H. multifidus* by smaller flowers, which remain slightly drooping.

Holotype: Slowenien, Istrien, Čičarija/Cicceria/Tschitschenboden, S Kozina/Cosina, am Weg von Podgorje/Piedimonte del Taiano auf den Berg Slavnik/M. Taiano/Slaunig, N 45°31,753', E 13°58,483', 885 m alt.; Waldrand; 14.05.2010; leg. V. Mikoláš, W. Mucher sen. & W. Starmühler (KL-Herbarium Istriacum).

Isotypes: GZU, LJU, M, W.

Syntype: Slowenien, Istrien, Čičarija/Cicceria/Tschitschenboden, S Kozina/Cosina, am Weg von Podgorje/Piedimonte del Taiano auf den Berg Slavnik/M. Taiano/Slaunig, N 45°31,185', E 13°58,179', 749 m alt.; Karstheide; 14.05.2010; leg. V. Mikoláš, W. Mucher sen. & W. Starmühler (KL-Herbarium Istriacum).

Eponymy: This new hybrid is dedicated to my father Walter Mucher sen. (nat. 26.03.1942) for his permanent support of my botanical work.

Helleborus dumetorum × ***H. odorus*** = ***Helleborus*** ×***tergestinus*** Starmühler 2007, Carinthia II 197./117.: 413.

This hybrid can be distinguished from *H. dumetorum* by hairy leaves with exserted veins and larger flowers with broad ovate tepals, and from *H. odorus* by leaves with more leaflets and by flowers with only broad ovate tepals.

Landesmuseum Kärnten
Kärntner Landesherbar (KL)
Phanerogamen

Inv.-Nr.: BP.............................

HERBARIUM ISTRIACUM

✣✣✣✣✣✣✣✣✣✣✣✣✣✣✣✣✣✣✣✣✣✣✣✣✣

Helleborus ×mucheri :Rottensteiner

(*H. dumetorum* × *H. multifidus*)

HOLO-TYPUS

SLOWENIEN, Istrien, Čičarija/Cicceria/Tschitschenboden, S Kozina/Cosina, am Weg von Podgorje/Piedimonte del Taiano auf den Berg Slavnik/M. Taiano/Slaunig, N 45°31,753‘, E 13° 58,483‘, 885 m alt.; Waldrand.

14.05.2010 leg. V. Mikoláš, W Mucher sen. & W. Starmühler
det. W. Starmühler

Fig. 11. Holotype specimen of *Helleborus ×mucheri* in the herbarium KL-Herbarium Istriacum.

Fig. 12. Lamina of a basal leaf of the holotype specimen of *Helleborus ×mucheri* in the herbarium KL-Herbarium Istriacum.

Specimina selecta: Italien, Triestino/Territorium von Triest, E Trieste/Triest, 0,15 km SE Padriciano/Padriče/Padrich, N 45°38,99', E 13°50,40', 365 m alt.; *Pinus nigra*-Wald; 17.03.2001; leg. W. Starmühler (GJO, GZU, IBF, KL, LJU, TSB, W, WHB, WU), Typen. – Italien, Triestino/Territorium von Triest, E Trieste/Triest, etwa 0,2 km NW Trebiciano/Trebče/Trebich, N 45°40,57', E 13°49,16', 340 m alt.; *Pinus nigra*-Wald; 17.03.2001; leg. W. Starmühler (GZU, KL, LG, LI, Herb. D.Koriakov/RU-Novosibirsk). – Italien, Triestino/Territorium von Triest, E Trieste/Triest, 0,5 km NE Basovizza/Bazovica/Basowitz, N 45°38,81', E 13°52,42', 380 m alt.; Trockenrasen; 17.03.2001; leg. W. Starmühler (KL).

Helleborus dumetorum* × *H. viridis

It differs from *H. dumetorum* by ± dispersed hairy leaves with exserted veins, and from *H. viridis* by yellowish green flowers, which remain slightly drooping.

Specimina selecta: Istrien, Abbazia; 02.04.1893; leg. J. Nevole (GZU).

Helleborus foetidus* × *H. niger* = *Helleborus ×sahinii Grimshaw 2000, Plantsman 9 (4): 231.

This hybrid can be distinguished from *H. foetidus* by its larger flowers, as well as by other intermediate characters, while from *H. niger* by its tooth-edged leaves and smaller flowers.

Helleborus foetidus* × *H. viridis* = *Helleborus ×jordanii Pages 1914, Bull. Acad. Int. Géogr. Bot. 24: 167.

This hybrid differs from *H. foetidus* by a few-leaved stem, larger leaves, slightly incised bracts, and inflorescence with fewer flowers. From *H. viridis* it differs by a leafy stem, smaller leaves, only slightly incised bracts, and inflorescence with more flowers.

Fig. 13. Inflorescence with young fruit of the holotype specimen of *Helleborus* ×*mucheri* in the herbarium KL-Herbarium Istriacum.

Helleborus niger* × *H. orientalis* = *Helleborus* ×*lemonnierae Demoly 2000, Bull. Assoc. Parcs Bot. France 30: 48.

The 2 main characteristics of this hybrid are the only slightly incised bracts (undivided in *H. niger*, but deeply incised in *H. orientalis*), and the mixture of the colour of the tepals.

Helleborus multifidus* × *H. odorus

This hybrid can be distinguished from *H. multifidus* by larger flowers with broad ovate tepals, and from *H. odorus* by leaves with more leaflets and by smaller flowers with broad ovate tepals.

Specimina selecta: Flora Italiae, TS, M.te die Pini (Padriciano), 300 m s.l.m.; 26.03.[20]02; leg. L. Poldini (TSB-028327, TSB-028328, TSB-028329, TSB-028330).

Helleborus multifidus* × *H. viridis

This hybrid can be distinguished from *H. multifidus* by leaves with fewer leaflets, and from *H. viridis* by smaller flowers with ovate to narrow ovate tepals.

Specimina selecta: Fiume; 02., 03.; leg. Noë (GJO-26981/4506).

Helleborus odorus* × *H. viridis

It differs from *H. odorus* by leaves with narrower leaflets and smaller flowers with more greenish tepals and larger fruits. From *H. viridis* it differs by leaves with broader leaflets and larger flowers with yellowish green tepals and smaller fruits.

Specimina selecta: Fiume, alte ... Straße gegen Castua; 02.-03.1906; leg. Vončina (GZU).

Key for determination of species

1. Leaves are coriaceous or semi-coriaceous; tepals are white or purple **2**

– Leaves are not coriaceous; teplas are green or yellowish **4**

2. Bracts are undivided, their margins are entire; tepals white. – Stem is not branched, usually without cauline leaves; leaves divided into 7-9 leaflets, hardy, dark green; flowers 5-8 (-9) cm broad. – Herbaceous perennials, 15-20 (-30) cm tall. – Light woods, forest edges, on humous soil. – (XII-) I-III ...... ***Helleborus niger*** – Black Hellebore, Christmas rose

> **a.** Leaflets are from broad lanceolate to obovate, rhomic, broadest in the terminal part, with the margin toothed at the apex; flowers 5-8 cm broad; tepals after anthesis greenish .... subsp. ***niger*** – Black Hellebore n.s.
>
> – Leaflets are lanceolate, broadest in the central part; the margin toothed or spiky toothed; flowers 7-9 (-11) cm broad; tepals after anthesis mostly violet .... subsp. ***macranthus*** – Bigflowered Hellebore

– Bracts divided into 3-5 segments, its margins serrate; tepals purple **3**

3. Leaves are semi-coriaceus, not hardy, divided into 7-11 leaflets; main and lateral veins are not exserted; flowers 4-5.5 cm broad. – Herbaceous perennials, 20-40 cm tall. – Light woods and forest edges, meadows, vineyards. – III-V .... ***Helleborus atrorubens*** – Dark Hellebore

– Leaves are coriaceous, hardy, divided into 7-11 leaflets; main veins and lateral veins are exserted; flowers 6-9 cm broad. – Herbaceous perennials, 20-60 cm tall. – Shibliak and light woods. – II-IV .... ***Helleborus orientalis*** – Oriental Hellebore

4 (1). Stem with many cauline leaves; bracts are not divided, ovate. – Leaves divided into 3-9 leaflets; leaflets narrow lanceolate; inflorescence with usually more than 10 flowers; flowers 1-2.5 (-3) cm broad, bell-shaped, ± drooping; tepals green with dark red margins; carpels 3 (-4). – Herbaceous perennials, 20-80 cm tall. – Light woods, forest edges and shibliak, on little dry to moist soil. – I-IV .... ***Helleborus foetidus*** – Stinking Hellebore

– Stem is without cauline leaves, rarely with 1 or 2; bracts divided into lanceolate segments **5**

5. Leaves are with hairy main veins; main veins are little exserted, lateral veins are not exserted. – Leaves are not hardy, divided into 7-11 (-13) leflets, the central 3 leflets always undivided, 1-3 cm broad, green to dark green; inflorescence with (2-) 3-5 (-6) flowers; bracts are divided; flowers 3-4 (-5) cm broad, ± drooping; tepals narrow-ovate, pale green, cup-shaped, 2.5-3.5 (-4) cm broad; carpels 3-5; ripe fruit 15-18 mm long (without beak). – Herbaceous perennials, 20-30 (-40) cm tall. – Karst heath, light woods, shibliak, mostly on moist soil. – III-IV .... ***Helleborus dumetorum*** subsp. ***illyricus*** – Illyrian Hellebore

– Leaves on the underside are hairy along the veins or on the whole lamina; all veins are dintinctly exserted **6**

6. Leaves are divided into 11-50 leaflets; inflorescence with 3-8 flowers, arranged vertically; flowers 3.5-5.5 cm broad; tepals are from broad-lanceolate to narrow-ovate. – Leaves are not hardy; carpels 3-6; flowers cup-shaped; tepals yellowish or pale green; ripe fruit 18-20 mm long (without beak). – Herbaceous perennials, 25-45 cm tall. – Shrubbery edges, light woods, shibliak, often in dry habitats, more often than all other species in this region. – II-IV .... ***Helleborus multifidus*** – Cleavedfoliated Hellebore

> **a.** Leaflets are less than 2 cm broad, mostly divided almost to the base, at the margin only distant and coarsely toothed .... subsp. ***multifidus*** – Cleavedfoliated Hellebore n.s.
>
> – Leaflets are more than 2 cm broad, some of them divided almost to the base, some only to the middle, at the margin more finely toothed .... subsp. ***istriacus*** – Istrian Hellebore

– Leaves are divided into 7-17 leaflets; inflorescence with 1-4 flowers, arranged almost horizontally; flowers 4-7 cm broad; tepals are from broad lanceolate to almost circular 7

7. Leaves are hardy, divided into 5-11 leaflets; leaflets from lanceolate to broad-lanceolate, 1.5-6 cm broad, veins thick, inflorescence with 2-4 flowers; flowers 5-7 cm broad; tepals almost circular, from yellowish to yellowish green; carpels (4-) 5; ripe fruit

15-20 mm long (without beak). – Herbaceous perennials, 30-50 (-60) cm tall. – Shrubbery edges, shibliak, light woods. – I-III .... ***Helleborus odorus*** – Fragrant Hellebore

a. Leaves are divided into 7-11 leaflets; leaflets are not incised .... subsp. ***odorus*** – Fragrant Hellebore n.s.

– Leaves are divided into 5-7 leaflets; leaflets are mostly incised to 2-5 segments .... subsp. ***laxus*** – Loose Hellebore

– Leaves are not hardy, divided into 7-17 leaflets; leaflets narrow-lanceolate, 1-2 cm broad, veins narrow; inflorescence with 1-3 (-4) flowers; flowers 4-5 cm broad; tepals broad-ovate, green; carpels 3-5; fruit 25-28 mm long (without beak). – Herbaceous perennials, 20-40 (-50) cm tall. – Shrubbery edges, shibliak, light woods, meadows. – II-IV .... ***Helleborus viridis*** subsp. ***viridis*** – Green Hellebore n.s.

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SOME NOTES ON THE GENUS *ACONITUM* IN CHORNOHORA MTS.

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Marina Ragulina [1]

Abstract. The paper is a contribution to ecology and chorology of *Aconitum* in high-mountain zone of the Ukrainian Carpathians. It was confirmed that genus *Aconitum* in the Chornogora mountain range is represented by 14 taxa, and 7 more taxa were listed as potential for this region. These taxa belong to 3 subgenera and are divided on 4 main biomorphological groups delimited on the base of their habitat, life form, ecology and altitudinal distribution. The soil and vegetation types for all taxa have been identified and the maps of their distribution have been prepared. The most influent threats and their categories were identified. Threat category for *A.* × *nanum* was changed from DD to VU, and for *A. firmum* subsp. *fussianum* from NT to VU.

Key words: *Aconitum*, Chornogora, sozology, ecology, chorology, soils, vegetation

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Introduction

The genus *Aconitum* L. (Ranunculaceae Juss.) is an interesting taxonomical group which is characterized by high level of morphological diversity, presence of a number of subspecific taxa, and high number of both infra- and interspecific natural hybrids (Gáyer 1922; Götz 1967; Seitz 1969; Seitz *et al.* 1972; Kadota 1981, 1987; Hoot 1991, 1995; Park *et al.* 1997; Mitka & Zemanek 1997; Mitka 2000, 2002, 2003, 2008; Starmühler 2001; Starmühler & Mitka 2001; Mitka & Szajna 2009; Новіков 2010a; Novikoff & Mitka 2011). The genus *Aconitum* during long time was not critically investigated in Ukrainian Carpathians, and as a result only two aggregated taxa (*A. anthora* and *A. lasiocarpum*) from this region have been included in Red Book of Ukraine in 2009 (Дідух 2009; Новіков 2010b, 2010c; Тасєнкевич *та ін.* 2011).

In the Carpathian Mountains one of the main centers of evolution and endemism of monkshoods in Europe is located (Mitka 2003; Новіков і Mitka 2011; Novikoff & Mitka 2011). For example, in Ukrainian Carpathians from total number (19 confirmed + 3 unconfirmed *Aconitum* taxa) 9 species and subspecies are listed as clearly endemic or subendemic and 2 more hybrid subspecies are considered as probably endemic (Novikoff & Hurdu 2015). From other side, if we consider all forms and varieties then we can tell about 17 subendemic and endemic taxa in general.

The Chornohora Mts. is the highest mountain range in Ukrainian Carpathians which is located on about 1270 km^2 area in Zakarpathia (Transcarpathia) and Ivano-Frankivsk regions (Fig. 1). These mountains are mostly consist of flysch that predetermines their comb-like relief. They are also characterized by high diversity of flora and vegetation and represent all vegetation belts: submontane (up to 600 m a.s.l.), lower montane (up to 1200 m a.s.l.), higher montane (up to 1550 m a.s.l.), subalpine (up to 1800 m a.s.l.), and alpine (up to 2061 m a.s.l.) (Чопик 1976, 1977; Стойко 1977; Малиновський 1980; Малиновский 1991; Малиновський і Крічфалушій 2000; Нестерук 2003; Новіков 2016).

It was showed that Chornogora Mts. is one of the most important center of diversity of monkshoods and include almost all

Tab. 1. Genus *Aconitum* in Ukrainian Carpathians. + – taxon confirmed during the last expeditions in 2008-2015; **?** – taxon is cited or suggested in literature, or there are herbarium vouchers but currently it is not confirmed by field expeditions; - – taxon is not known from this region. ►

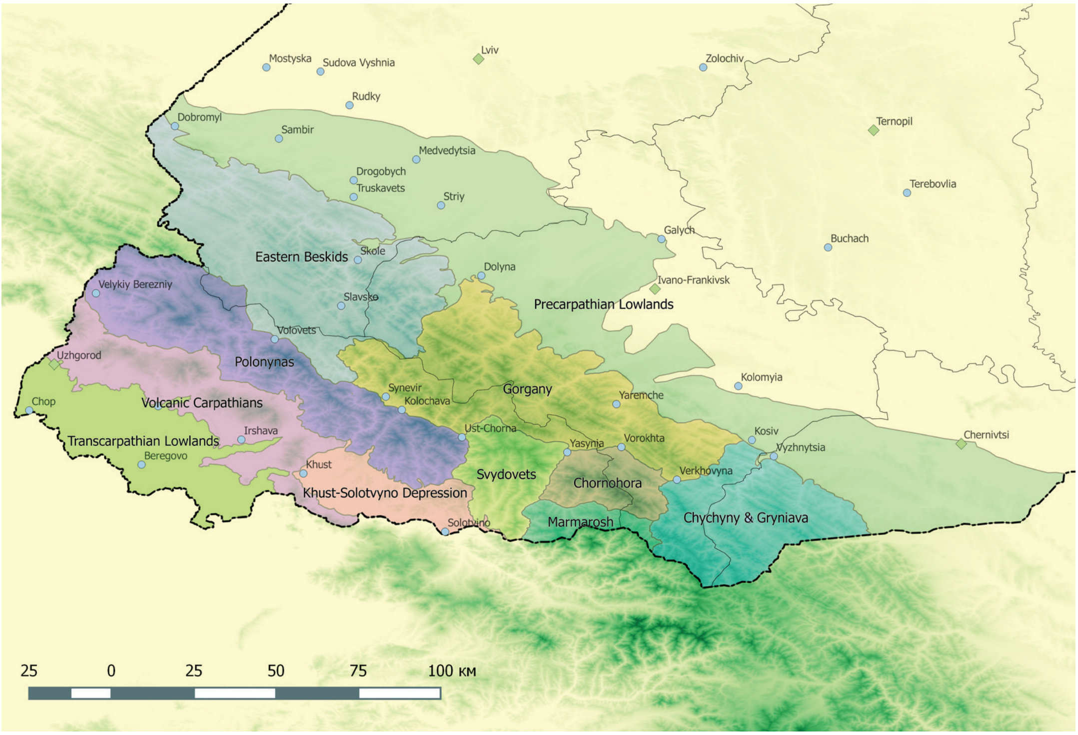

Fig. 1. Division of Ukrainian Carpathians (Novikoff & Hurdu 2015).

Aconitum taxa of the Ukrainian Carpathians (19 confirmed and 3 suggested) from which 16 are considered as endemic or subendemic and 10 – as threatened (Tab. 1) (Новіков 2010b, 2010c; Новіков 2016). Taking also into consideration that about 39,2% of the Chornogora area is under protection (Fig. 2), investigations of the genus in this territory is an important task.

Detailed descriptions of the taxa and the keys for their identification, as well as discussion on general chorology, can be found in our previous works (Mitka 2003, 2008; Новіков 2009, 2010b, 2011a, 2011b, 2013, 2016; Новіков і Mitka 2011; Mitka & Novikoff 2011; Novikoff & Mitka 2011). Here we are focusing on diversity, distribution, phytocoenotic and habitat properties, ecology, and protection of monkshoods in the Chornogora.

Material and methods

Preliminary analysis has been realized conducted on the base of field expeditions during 2008-2014. In 2015 special expedition to Chornohora with aim to evaluate main ecological parameters in known and to describe releves, as well as to find new habitats were realized by one of us (A. Novikoff). As a result, 26 localities (Apps. 1-3) were precisely analyzed.

Vegetation description follows the Braun-Blanquet method and quadrates of about 25 m^2. The following abundance scale coefficients was applied: r – 1 or very few plants; + – few

Taxon	Threat Category	Endemic Status	Occurrence in Ukrainian Carpathians	Occurrence in Chornohora
Subg. *Aconitum*				
Sect. *Aconitum*				
A. bucovinense Zapał. fo. *bucovinense*	EN	South-Eastern Carpathian endemic	+	+
A. bucovinense Zapał. fo. *orthotricha* Gáyer	EN	South-Eastern Carpathian endemic	+	+
A. × *czarnohorense* (Zapał.) Mitka	VU	Eastern Carpathian endemic	+	+
A. firmum Rchb. subsp. *firmum*	VU	Pan-Carpathian endemic	+	?
A. firmum Rchb. subsp. *fissurae* Nyárády	VU	Pan-Carpathian endemic	+	+
A. firmum Rchb. nothosubsp. *fussianum* Starmühl.	VU	Pan-Carpathian endemic	+	?
A. × *nanum* (Baumg.) Simonk.	VU	South-Eastern Carpathian endemic	+	+
Sect. *Cammarum* DC.				
A. variegatum L. subsp. *variegatum*	DD	none	?	?
A. variegatum L. subsp. *podobnikianum*	DD	none	?	?
A. lasiocarpum (Rchb.) Gáyer subsp. *lasiocarpum*	VU	Eastern Carpathian endemic	+	?
A. lasiocarpum (Rchb.) Gáyer subsp. *kotulae* (Pawł.) Starmühl. & Mitka	VU	Pan-Carpathian subendemic	+	?
A. degenii Gáyer subsp. *degenii* fo. *degenii*	LC	Pan-Carpathian endemic	+	+
A. degenii Gáyer subsp. *degenii* fo. *craciunelense* Gáyer	LC	Pan-Carpathian endemic	+	+
A. degenii Gáyer subsp. *degenii* var. *intermedium* (Zapał.) Mitka	LC	Pan-Carpathian endemic	+	+
A. × *gayeri* Starmühl.	LC	Eastern Carpathian endemic	+	+
Sect. *Acomarum* Starmühl.				
A. ×*cammarum* L. em. Fries	LC	none	+	+
Subg. *Anthora* (DC.) Peterm.				
Sect. *Anthora* DC.				
A. anthora L.	VU	none	+	+
Subg. *Lycoctonum* (DC.) Peterm.				
Sect. *Lycoctonum* DC.				
A. lycoctonum L. em. Koelle subsp. *lycoctonum*	DD	none	?	?
A. moldavicum Hacq. subsp. *moldavicum*	LC	Pan-Carpathian subendemic	+	+
A. moldavicum Hacq. subsp. *hosteanum* (Schur) Graebn. & P. Graebn.	LC	Pan-Carpathian subendemic	+	+
A. moldavicum Hacq. nothosubsp. *simonkaianum* (Gáyer) Starmühl.	DD	Eastern Carpathian (sub) endemic	+	+
A. moldavicum Hacq. nothosubsp. *porcii* Starmühl.	DD	South-Eastern Carpathian and Bihor endemic	+	-

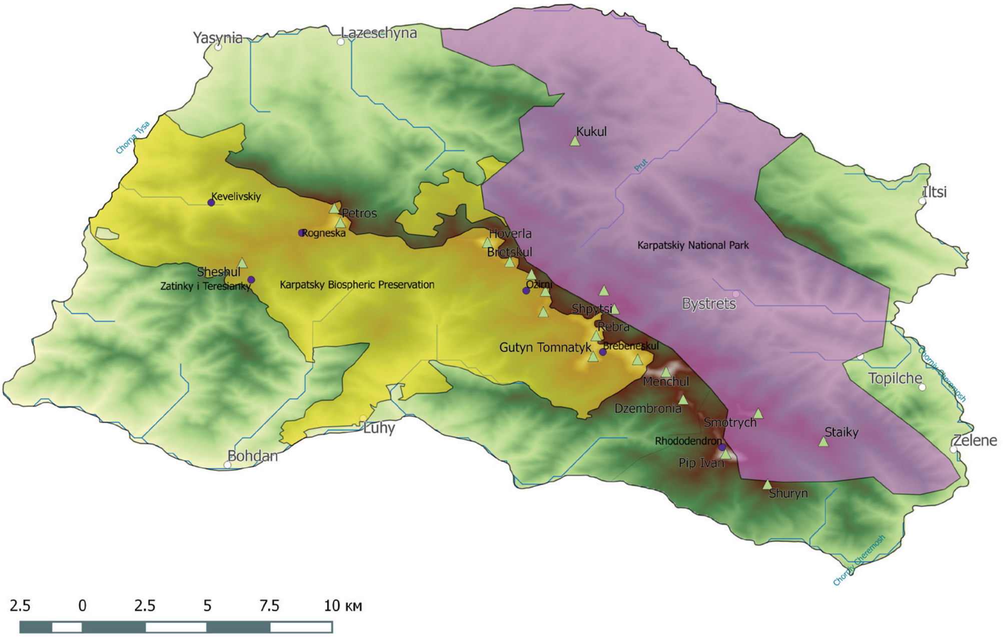

Fig. 2. General map of Chornohora and its protected areas. **Triangles** – the highest peaks; **white circles** – settlements; **blue circles** – local sanctuaries and nature monuments.

plants with slight covering; 1 – < 5% of covering with numerous plants; 2m – ~ 5% of covering; 2a – 6-12% of covering; 2b – 13-25% of covering; 3 – 26-50% of covering; 4 – 51-75% of covering; 5 – >75% of covering (Wikum & Shanholtzer 1978; Westhoff & van der Maarel 1978; Dietvorst *et al.* 1982). Identification of vegetation communities was realized on the base of several sources (Малиновський 1980; Matuszkiewicz 2001; Snowarski 2002-2016; Tasenkevich *et al.* 2011).

For each of the local populations the extent of anthropogenic pressure and general condition (bad, normal, good, and prosperous) were recognized. The mean or, if it was possible, strict number of pregenerative, generative and postgenerative plants in each of populations were calculated. On the base of these calculations, the class of population vitality was identified following Mirkin (Миркин и др. 2001) criteria: a) invasive – pregenerative plants predominate; b) normal – generative plants predominate; c) regressive – postgenerative plants predominate. Density and general area of population were also taken into account.

Measurements of soil parameters were made just near the plants, on depth of about (5)18-20 cm. Soil temperature was analyzed by Ezodo MP-103S, and soil moisture – by Rixen M-700S. Air temperature, air relative humidity, Illumination, and wind speed were analyzed by multifunctional tool Flus ET-965. Soil pH and superficial soil moisture were measured in laboratory on the base of collected soil samples. Superficial soil moisture was calculated by standard gravimetric method. A profile-genetic principle adopted for the WRB nomenclature was applied for soils classification (IUSS Working Group WRB 2006).

Next ecological categories were applied (Дідух *та ін.* 2000; Новіков і Барабаш-Красни 2015). For illumination: a) sciophytes – plants grow in shady places; b) helio-sciophytes – plants prefer shady places but also tolerate bright sunlight; c) scio-heliophytes – plants prefere bright sunlight but also tolerate partial shade; d) heliophytes – plants grow on open places under bright sunlight. For soil acidity: a) hyperacidophils – grow on the substrates with ph < 3,7; b) peracidophils – pH = 3,7-4,5; c) acidophils – pH = 4,5-5,5; d) subacidophils – pH = 5,5-6,5; e) neutrophils – pH = 6,5-7,0; f) basiphils – pH = 7,0-8,0; g) hyperbasiphils – pH > 8,0. For water relation: a) hydrophytes – aquatic plants; b) helophytes – partially aquatic, partly submerged or littoral plants; c) hygrophytes – plants living in moist habitats; d) hygro-mesophytes – plants intermediate between hygro- and mesophytes; e) mesophytes – plants which are adapted to moderate moisture; f) meso-xerophytes – plants intermediate between meso- and xerophytes; g) xerophytes – plants adopted to dry environment.

Maps are built in QGis Wien 2.8.2 on the base both of literature and herbarium data, as well as own field observations. In case of literature and herbarium data the points are given for nearest identified place that is pointed in the source.

Threat categories by IUCN (2015) are given on the base of our previous studies (НОВІКОВ 2010b, 2010c; НОВІКОВ І МИТКА 2011; MITKA & NOVIKOFF 2011; NOVIKOFF & MITKA 2011) completed with new obtained data.

Results

A. bucovinense

Ecological preferences: Heliophytes, rarely – scio-heliophytes; mesophytes or meso-xerophytes, rarely – hygro-mesophytes; peracidophils or acidophils.

Distribution and habitats in Ukrainian Carpathians: In Ukrainian Carpathians are known only few confirmed localities in Chornohora, Chyvchyny, Gorgany and Eastern Beskids. This species is mostly associated with higher montane and subalpine belts, however also occurs in alpine and lower montane belts. These plants grow mostly on open places in tall-herb communities, on screes, in rock cracks, sometimes in ecotones with shrubs or just inside of the crown of low shrubs in subalpine and alpine belts. They also could be found along the streams and near mountain lakes. The species take a part in several communities – *Juniperetum sibiricae, Pulmonario-Alnetum viridis, Pinetum mughi,* and *Poo-Deschampsietum*.

Distribution and habitats in Chornogora: There are confirmed only two isolated mixed populations near Petrosul Mt. and on the saddle between Pozhyzhevska Mt. and Breskul Mt. (Fig. 3; Apps. 1-3, entries 4, 5 and 9). In general these populations are in normal condition, but consist of less than 100 plants and cover less than 1 km^2 of area. Generative plants there dominated and, as a result, populations could be identified as belonging to normal class of vitality. In Chornogora the species is known from *Poo-Deschampsietum*, and *Juniperetum sibiricae* communities on leptic cambisols and umbric gleysols.

Threats: The overgrowing by woody plants and changes in the hydrological regime of habitats, as well as trampling by tourists. For Ukrainian Carpathians in general it could be designated as EN.

A. firmum

Ecological preferences: Heliophytes or scio-heliophytes; hygro-mesophytes, mesophytes or rarely meso-xerophytes; peracidophils or acidophils, rarely – hyperacidophils or subacidophils.

Distribution and habitats in Ukrainian Carpathians: This species is rare for Ukrainian Carpathians, where is mostly represented in Chornohora and Svydovets but also sporadically occurs in Gorgany, Polonynas, Marmarosh and Chyvchyny. It is mostly related to alpine and subalpine belts, but also occurs in higher and lower montane belts. There it grows in tall-herb communities, on stone screes, in rock cracks, sometimes in ecotones with shrubs or just inside of the crown of low shrubs in subalpine and alpine belts. They also could be found along the streams and near mountain lakes. The species take a part in *Poo-Deschampsietum, Aconitetum firmi, Ranunculo platanifolii-Adenostyletum alliariae, Caricetum sempervirentis,* and *Juniperetum sibiricae* communities.

Distribution and habitats in Chornogora: In Chornohora only subsp. fissurae is confirmed during our own observations, but there are herbarium vouchers of other two subspecies from this region too. There are confirmed three mixed populations on Petros Mt., Turkul Mt., and near the lake Brebeneskul in good and prosperous conditions. However we found also one isolated population on slopes of Goverla Mt., which is in extremely bad condition and represented by just few postgenerative plants (Fig. 4; Apps. 1-3, entries 1, 14, 15 and 22). In general *A. firmum* in Chornogora is represented by ~1000 plants predominantly in pregenerative and generative condition (normal class of vitality) which cover about 1-2 km^2. In Chornohora this species is registered in *Poo-Deschampsietum, Aconitetum firmi, Ranunculo platanifolii-Adenostyletum alliariae, Caricetum sempervirentis,* and *Juniperetum sibiricae* communities on cambic leptosols, umbric or mollic gleysols and leptic cambisols.

Threats: In general, this species is very rare for Chornogora Mts. and requires protection due to the intense burning and trampling of its habitats by tourists. In Ukrainian Carpathians it has VU category.

A.* × *czarnohorense

Ecological preferences: Heliophytes, rarely – scio-heliophytes; mesophytes or meso-xerophytes, rarely – hygro-mesophytes; acidophils, rarely – peracidophils or subacidophils.

Distribution and habitats in Ukrainian Carpathians: The species occurs very often in Chornohora Mts., but it also grows in Svydovets, Gorgany, Polonynas and Marmarosh Mts. It very often occurs in mixed populations with *A. firmum, A.* × *nanum* and sometimes – with *A. bucovinense.* It is usually related to alpine and subalpine belts, but also occurs in higher montane belt. These plants grow on stone screes, in cracks of the rocks, in natural depressions and low cavities, and sometimes occur near the streams and high-mountain lakes. The species take a part in *Pulmonario-Alnetum viridis, Juniperetum sibiricae, Pinetum mughi, Caricetum sempervirentis, Aconitetum firmi, Primulo-Caricetum curvulae,* and *Poo-Deschampsietum* communities.

Distribution and habitats in Chornogora: In Chornogora Mts. the species has a center of distribution and is represented here by five main local mixed populations in good and prosperous condition – on mountains Petros, Gutyn-Tomnatyk, Brebeneskul, Menchul, and near the lake Brebeneskul (Fig. 5; Apps. 1-3, entries 1, 2, 15, 16, 24, and 25). The most of plants are in pregenerative and generative stages; therefore vitality of these populations is normal. In general *A.* × *czarnohorense* here includes about 2000 plants which cover more than 5 km^2. In Chornohora this species is registered in all of mentioned above communities on cambic leptosols, umbric or mollic gleysols and leptic cambisols.

Threats: This species is represented on Chornogora in enough amounts but nevertheless it needs a protection because it grows mostly on the touristic paths and near the camping places. Among other threats the overgrowing of habitats by shrubs. In Ukrainian Carpathians it has VU category.

A.* × *nanum

Ecological preferences: Heliophytes, rarely – scio-heliophytes; mesophytes or meso-xerophytes, rarely – hygro-mesophytes; acidophils, rarely – peracidophils or subacidophils.

Distribution and habitats in Ukrainian Carpathians: The one of the most distributed high-mountain monkshoods in Eastern Carpathians. In Ukrainian Carpathians it occurs in Chornohora, Svydovets, Gorgany, Marmarosh, as well as in Polonynas and Eastern Beskids. The plats very often grow in mixed populations together with *A. firmum, A.* × *czarnohorense* and sometimes – with *A. bucovinense*. The species is related to alpine and subalpine belts, but also occurs in higher montane belt. These plants grow on stone screes, in cracks of the rocks, in natural depressions and low cavities, and sometimes occur near the streams and high-mountain lakes. The species take a part in numerous communities such as *Pulmonario-Alnetum viridis, Juniperetum sibiricae, Pinetum mughi, Caricetum sempervirens, Aconitetum* *firmi, Ranunculo platanifolii-Adenostyletum alliariae, Primulo-Caricetum curvulae,* and *Poo-Deschampsietum*.

Distribution and habitats in Chornogora: Together with *A.* × *czarnohorense* it is one of the most distributed high-mountain *Aconitum* species in Chornogora. There are known several main mixed populations on mountains Petros and Brebeneskul, as well near the lake Brebeneskul which consist of about 1000-1500 plants of mostly pregenerative and generative age, and which cover about 2 km^2 (Fig. 6; Apps. 1-3, entries 1, 15, and 24). Mentioned populations are in good and prosperous conditions with normal vitality. In Chornogora the species is known from *Caricetum sempervirens, Aconitetum firmi, Ranunculo platanifolii-Adenostyletum alliariae*, and *Poo-Deschampsietum* communities on cambic leptosols and umbric or mollic gleysols.

Threats: Trampling by tourists, burning of habitats, overgrowing of habitats by woody plants. In Ukrainian Carpathians it has VU category and together with *A. firmum, A.* × *czarnohorense* and *A. bucovinense* requires strict protection.

A. variegatum

Ecological preferences: Scio-heliophytes or helio-sciophytes; hygrophytes or hygro-mesophytes, rarely – mesophytes; probably subacidophils (Дідух *та ін.* 2004).

Distribution and habitats in Ukrainian Carpathians: There are mentions of this species from the region of the lake Synevyr in Zakarpatia region (Gorgany Mts.) (Новіков і Мітка 2011), however they are still not confirmed. The only specimen of *A. variegatum* from Ukrainian Carpathians (Chornohora) is deposited in herbarium of Ivan Franko National University of Lviv (LW). Nevertheless, this species in Ukraine is known from lower altitudes in Volhynia and Ciscarpathia. Probably it could be found in submontane or lower montane belts in such communities as *Alnetum incanae* and *Arunco-Doronicetum*.

Distribution and habitats in Chornogora: The species is not confirmed for Chornohora Mts. The approximate location of abovementioned specimen (LW, Woloszczak E., 17.08.1888) is shown on Fig. 7.

Threats: Due its unclear chorology – DD.

A. lasiocarpum

Ecological preferences: Scio-heliophytes or helio-sciophytes; hygrophytes or hygro-mesophytes, rarely – mesophytes; probably subacidophils (Дідух *та ін.* 2004).

Distribution and habitats in Ukrainian Carpathians: The species is mostly distributed in Western and Eastern Carpathians, but also sporadically occurs in Southern Carpathians and related lowlands. In Ukrainian Carpathians it is mostly represented in Eastern Beskids while in other regions it occurs irregularly and rarely. The presence of the species in Eastern Beskids and Chyvchyny Mts. is confirmed by own observations, while the presence of it in Marmarosh, Gorgany and Svydovets Mts. requires further validation. In Eastern Beskids the species is distributed mostly in submontane and lower montane belts while in Chyvchyny Mts. it was observed in upper montane and subalpine belts. These plants grow mostly in semi-shady places, between shrubs and at the forest edges. Very often they occur near the water. However in Chyvchyny Mts. the plants grow in open and dry place, in subalpine herbal communities. As a result, these plants differ by their common habitus. They are high and branched in lower altitudes, and compact with few flowers – in higher altitudes. In general, the species is known from *Alnetum incanae, Carici remotae-Fraxinetum, Dentario glandulosae-Fagetum, Trollio-entauretum, Adenostylion, Calthion*, and *Carpinion* communities.

Distribution and habitats in Chornogora: There are known several specimens collected from Chornohora Mts (Fig. 8). Also there are known one population from neighborhoods of Vorokhta village. However current condition of all these populations is unknown. Today this species seems to be absent or very rare for Chornohora Mts.

Threats: This species is protected by Bern Convention and included to the Red Book of Ukraine (Мельник і Баточенко 2009) too. In general it can be evaluated as vulnerable taxon which requires strict protection on whole territory of Ukrainian Carpathians. The probably threats are hydrological changes and deforestations (Мельник і Баточенко 2009).

A. degenii

Ecological preferences: Scio-heliophytes or helio-sciophytes; hygrophytes or hygro-mesophytes, rarely mesophytes, or very rarely hygro-helophytes; peracidophils, acidophils or subacidophils.

Distribution and habitats in Ukrainian Carpathians: In Ukrainian Carpathians the species is represented by only one subspecies – *A. degenii* subsp. *degenii* which includes two forms (fo. *degenii* and fo. *craciunelense*) and one variety (var. *intermedium*). The last one coresponds to *A.* × *hebegynum*, taxonomical status of which was revised and then decreased (Ilnicki & Mitka 2011). This taxon is widely distributed in Ukrainian Carpathians up to subalpine or even alpine belt. It can be often found along the streams, near the lakes, in wet meadows, both in open and semi-shaded places. It mostly grow in large mixed populations together with *A.* × *gayeri*. This taxon is confirmed for Chornohora, Chyvchyny, Gryniava, Eastern Beskids, Gorgany, Marmarosh, Svydovets, and Volcanic Carpathians. It takes a part in a lot of communities including *Juniperetum sibiricae, Vaccinio myrtilli-Pinetum mughi, Phleo alpini-Deschampsietum caespitosae, Carici remotae-Fraxinetum, Alnetum incanae, Calthetum laetae, Caltho-Alnetum, Dentario glandulosae-Fagetum allietosum*, and *Ranunculo platanifolii-Adenostyletum alliariae*.

Distribution and habitats in Chornogora: In Chornohora Mts. this species very often occurs from submontane up to subalpine belt. There are confirmed 10 local populations which include about 2000 plants (Fig. 9; Apps. 1-3, entries 4, 5, 10-13, 17-21, 23). These populations are represented mostly by pregenerative and generative plants and are in general in good condition with normal or invasive type of vitality. In Chornohora Mts. this species mostly is represented in *Juniperetum sibiricae, Vaccinio myrtilli-Pinetum mughi, Phleo alpini-Deschampsietum caespitosae, Calthetum laetae, Ranunculo platanifolii-Adenostyletum alliariae,* and *Calthion* communities on haplic fluvisols and leptic cambisols.

Threats: As a result of wide distribution the species is considered as LC taxon. However there are also threats which can reduce the number of *A. degenii* plants. Among them – changes in hydrological conditions, water clogging by domestic waste, deforestations, and floods which destroys the vegetation cover.

A. × *gayeri*

Ecological preferences: Scio-heliophytes or helio-sciophytes; hygrophytes or hygro-mesophytes, rarely – mesophytes or sometimes hygro-helophytes; acidophils or subacidophils.

Distribution and habitats in Ukrainian Carpathians: Together with *A. degenii* it is one of the most usual monkshood in Ukrainian Carpathians, which is mostly distributed in submontane and lower montane belts of Chornohora, Chyvchyny, Gryniava, Eastern Beskids, Gorgany, Marmarosh, Svydovets, as well as Volcanic Carpathians and Polonynas. These plants similarly grow along the streams, near the lakes, in wet meadows, both in open and semi-shaded places. They are represented in the same communities as *A. degenii*.

Distribution and habitats in Chornogora: This species is represented in mixed populations with *A. degenii* and is very similar with it. Therefore it is not easy to clearly evaluate the total quantity, which is approximately about 1000 plants. For this research *A.* × *gayeri* was evaluated from 2 local populations in good condition (Fig. 10; Apps. 1-3, entries 11, 12, and 19). The most of the plants are in pregenerative and generative condition, while the general vitality of populations can be evaluated as normal. These plants are represented in *Carici remotae-Fraxinetum, Alnetum incanae, Calthion,* and *Adenostylion* communities on haplic fluvisols.

Threats: Similarly to *A. degenii* it is LC taxon. The main threats are changes in hydrological conditions, water pollution by domestic waste, deforestations, and floods which destroys the vegetation cover.

A.* × *cammarum

Ecological preferences: Scio-heliophytes or helio-sciophytes; hygro-mesophytes or mesophytes, rarely – meso-xerophytes; subacidophils or neutrophils.

Distribution and habitats in Ukrainian Carpathians and Chornogora: This is an ornamental species which is regularly planted near houses in the most of villages.

Threats: This taxon is not threatened.

A. anthora

Ecological preferences: Heliophytes or scio-heliophytes; xerophytes or meso-xerophytes, rarely – mesophytes; basiphils or neutrophils, rarely – hyperbasiphils or subacidophils.

Distribution and habitats in Ukrainian Carpathians: This is one of the rarest monkshoods in Ukrainian Carpathians which is sporadically represented on different altitudes from lower montane up to beginnings of alpine belts. This species is confirmed for Chornohora, Chyvchyny, Gryniava, and Eastern Beskids. It also known from Marmarosh Mts., and there are few herbarium specimens from Svydovets. These plants mostly grow on open xerothermic spaces between stones or just on the rocks, sometimes they occur among the short grasses or near the shrubs of alder, juniper or pine. From other side, the population from Stinka Mt. (Eastern Beskids) is located on rocks directly in shady forest.

Distribution and habitats in Chornogora: Several localities are usually mentioned for Chornohora, but we found only one of them. This population is located on the slopes of Petrosul and Petros Mts (Fig. 11; Apps. 1-3, entries 4 and 5). It includes only about 20 generative plants and can be classified as of normal vitality. However the general condition of the population seems to be bad because it is overgrowing by woody plants. Its communities can be determined as *Juniperetum sibiricae* or *Pulmonario-Alnetum viridis.* Soil type is subacidic leptic cambisol.

Threats: Overgrowing by tall herbs and woody plants.

A. lycoctonum

Ecological preferences: Sciophytes or helio-sciophytes; hygrophytes or hygro-mesophytes, rarely – hygro-helophytes; probably subacidophils (Дідух *та ін.* 2004).

Distribution and habitats in Ukrainian Carpathians and Chornogora: Presence of this species in Ukrainian Carpathians is under question. In general this species prefer *Tilio-Carpinetum* and *Adenostylion* communities in lower altitudes. There are some reports about its occurrence in Chornohora on the slopes of Pozhyzhevska Mt. (road from Zarosliak station to High-Mountain Station of Institute of Ecology of Carpathians; see Fig. 12). We inspected abovementioned plants, however they are not blooming and therefore we cannot undoubtedly identify them.

Threats: Confirmation of this taxon for Ukrainian Carpathians is needed.

A. moldavicum

Ecological preferences: Sciophytes or helio-sciophytes; hygrophytes or hygro-mesophytes, rarely – hygro-helophytes; from basiphils up to hyperacidophils.

Distribution and habitats in Ukrainian Carpathians: These plants are widely distributed in Ukrainian Carpathians, especially on low altitudes; however they also occur up to subalpine belt. They prefer wet and semi-shaded locations, especially in forests along the streams. However they also can be found on open places far away from water. The last plans differ by short and compact habitus, mostly ortotropic position of the shoot, lower number of flowers in unbranched or very slightly branched inflorescences, as well as more dark color of flowers. These plants have the widest ecological amplitude and very often can be found along the roads, in mountain villages, in forest fringes etc. From other side, this species do not make big populations with numerous plants, mostly there are few plants separated by comparatively big distances. In Ukrainian Carpathians this species occurs in all regions. In general there are information about participation of *A. moldavicum* in *Pulmonario-Alnetum viridis, Juniperetum sibiricae, Calthetum* *laetae,* and *Ranunculo platanifolii-Adenostyletum alliariae* communities.

Distribution and habitats in Chornogora: In Chornohora Mts. this species is mostly represented by subsp. *moldavicum* and subsp. *hosteanum* which form a lot of small local populations (Fig. 13; Apps. 1-3, entries 3-8, 11, 12, 17, 18, 20, 21 and 26). These two subspcies commonly are represented by several hundreds of generative and postgenerative plants. The condition of most populations is bad or near the normal because of low number of plants. They can be classified as regressive or rarely normal. These plants take a part in such communities as *Pulmonario-Alnetum viridis, Juniperetum sibiricae, Calthetum laetae, Ranunculo platanifolii-Adenostyletum alliariae,* and *Calthion*. They grow on very different soils including cambic leptosols, leptic cambisols, haplic cambisols, calcic fluvisols, and haplic fluvisol. There are also herbarium vouchers of nothosubsp. *porcii* from this region. However neither nothosubsp. *porcii* nor nothosubsp. *simonkaianum* (which probably could be refind too) were not confirmed during our expeditions on Chornohora.

Threats: Confirmation of nothosubsp. *porcii* and nothosubsp. *simonkaianum* for Chornohora is needed. There are no special threats for this species and there no need for its protection in Chornohora. As it seems small populations, low number of plants with presence of long-lived senile individuals is a normal condition for this species.

Discussion

In general, the genus *Aconitum* in Chornogora, such as in the in all Ukrainian Carpathians, includes four main biomorphological groups which have different ecological and altitudinal preferences, morphological features and also demonstrate different life forms (Новиков 2010a; Novikoff & Mitka 2011).

The fist biomorphological group is represented by subg. *Lycoctonum* and includes semi-rosette semi-orthotropic or plagiotropic plants which mostly are distributed in lower altitudes and prefer semi-shaded and wet forest habitats. We have ascertained these plants before as mesophytes (Novikoff & Mitka 2011) but these studies demonstrated that they are usually hygro-mesophytes or rarely hygrophytes. They have the widest ecological optimums can grow in very different soils.

Second group is represented by the diploid (sect. *Cammarum*) or triploid (sect. *Acomarum*) erosulate plants which prefer mostly open or rarely semi shaded habitats in montane zone. These plants were characterized before as mesophytes (Novikoff & Mitka 2011). However our current studies in Chornohora showed that they are rather hygro-mesophytes or even hygrophytes preferring the habitats along the open streams and wet meadows. This is erosulate orthotropic or semi-orthotropic plants. They are not so exposed to winds and therefore can grow higher, developing elongated (sometimes up to 2 m of high) branched shoots with ramified inflorescences.

Members of the subg. *Aconitum* sect. *Aconitum* are tetraploidic arctic-alpine plants (Hultén 1937) prefered open habitats (Mitka *et al.* 2007). These are mesophytes or meso-xerophyes adapted to oligothermic conditions of subalpine and alpine belts, only in some cases occurring in lower altitudes. These plants are not so depended from water sources like members of sect. *Cammarum*, but they also very often could be found along the streams and near the high-mountain lakes. They have strong, short and compact orthotropic erosulate shoots and mostly condensed inflorescences mostly because the higher plants have the higher risk to be destroyed by winds or hails. The most interesting adaptation of these plants against the stormy winds in alpine and subalpine belts is their integration in clumps of shrubs which protect them also against of freezing in winter and mechanical destruction.

Fourth group includes the only species *A. anthora* from subg. *Anthora*. These are xerophytic or meso-xerophytic plants with wide altitudinal range of distribution. These plants prefer open warm habitats, and in fact can be identified as xerothermic relicts (Hegi 1912). However they also could be found in shaded forest localities (i.e. on Stinka in Eastern Beskids) which probably are the second habitats for these plants. They are also erosulate and mostly orthotropic plants. The most interesting point about *A. anthora* is that it combines different features from other biomorphological groups (Novikoff & Mitka 2011). Currently we ascertained that *A. anthora* in Chornohora is growing on subacidic leptic cambisol while before it was strongly suggested that this plans are calciphilic petrophyls (Дідух *та ін.* 2004; Кобів 2010). This is of special interest because the Chornohora is mostly constructed from uncarbonated flysches which determine the development of short profiles of acidic soils (Нестерук 2003) and there are no open calcareous rocks like in Chyvchyny Mts. There are mostly acidic cambisols, leptosols or regosols, which however could be partly neutralized by salts containing in subterranean or piestic waters (Скиба *та ін.* 2006). As a result, specific vegetation which prefers more neutral conditions is mostly organized along the streams or has island type of distribution near the very local outcrops.

Many monkshoods play important role in mountain riparian ecosystems (Andersson *et al.* 2000; Le Cadre *et al.* 2008; Šibíková *et al.* 2008; Čarni & Matevski 2010; Pielech 2015). However, occurrence of the monkhoods along the streams and rivers in mountains, beside of water availability, is seems to be correlating with several other factors: a) watercourses form the natural landscape depressions covering the plants and protecting them from unfavorable weather conditions; b) water wash out the number of minerals including calcium from bedrocks and therefore along the torrents appear so called "island habitats" (Кобів 2007) with more neutral soils containing less organic material; c) in montane belt the sloped banks of rivers crossing the forests are more or less open and sunny localities with significantly fewer tree cover; d) such water flows serve as excellent spreading agents for dispersion of seeds (Cappelletti & Poldidni 1984; Danvind & Nilsson 1997) and even serve for vegetative propagation of monkshoods to lower elevations, and as a result – for occupation of new sites.

Conclusions

1. Our long-term field studies combined with herbarium investigations showed that the genus *Aconitum* in Chornogora is represented by 14 taxa belonging to 3 subgenera – *Aconitum* (sect. *Aconitum* – 5 taxa, sect. *Cammarum* – 4 taxa, and sect. *Acomarum* – 1 taxon), *Anthora* (sect. *Anthora* – 1 taxon), and *Lycoctonum* (sect. *Lycoctonum* – 3 taxa). 7 more taxa were pointed as potential for this region.
2. Detailed studies of current condition of local populations in Chornogora and comparison of them with both our observations from previous years and studies on herbarium collections allow us to identify most important threats for all of taxa and to clarify threat category for *A.* × *nanum* (it was changed from DD to VU), and for *A. firmum* subsp. *fussianum* (it was changed from NT to VU). As a result, for Ukrainian Carpathians in general, 10 taxa from 19 totally confirmed were ascertained as threatened. 3 more taxa are listed as those that can be potentially found in this region.
3. This study allowed clarifying ecological preferences of *Aconitum* taxa listed for the Chornogora Mts. in Ukrainian Carpathians. It was shown that the most of taxa have more or less wide ecological amplitudes (i.e. altitudinal distribution, relation to illumination, relation to soil acidity and soil moisture), and can grow in different communities. However we can conclude, as it was suggested before, that there are four main biomorphological groups which correspond to main sections of the genus and represent their general ecological preferences.
4. Other ecological parameters as air temperature, air humidity, illumination and wind speed etc. require more long-term investigations with application of datalogers. However obtained results could also be useful and applied further as a starting point.
5. Association *Aconitetum firmi* Pawł., Sokoł. et Wall. 1927 was described for the first time for the Ukrainian Carpathians. It is located near the lake Brebeneskul on Chornogora mountain range and includes *A. firmum*, *A.* × *nanum*, and *A.* × *czarnohorense*.

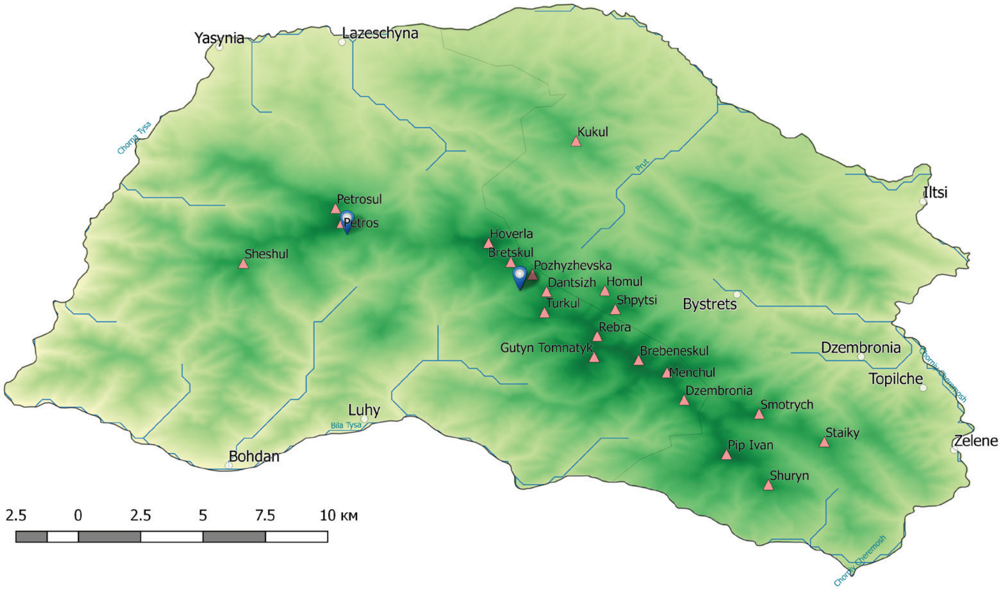

Fig. 3. Distribution of *A. bucovinense* in Chornohora Mts. **Blue points** – locations confirmed during expeditions; **red points** – locations known only from the herbarium collections and/or literature.

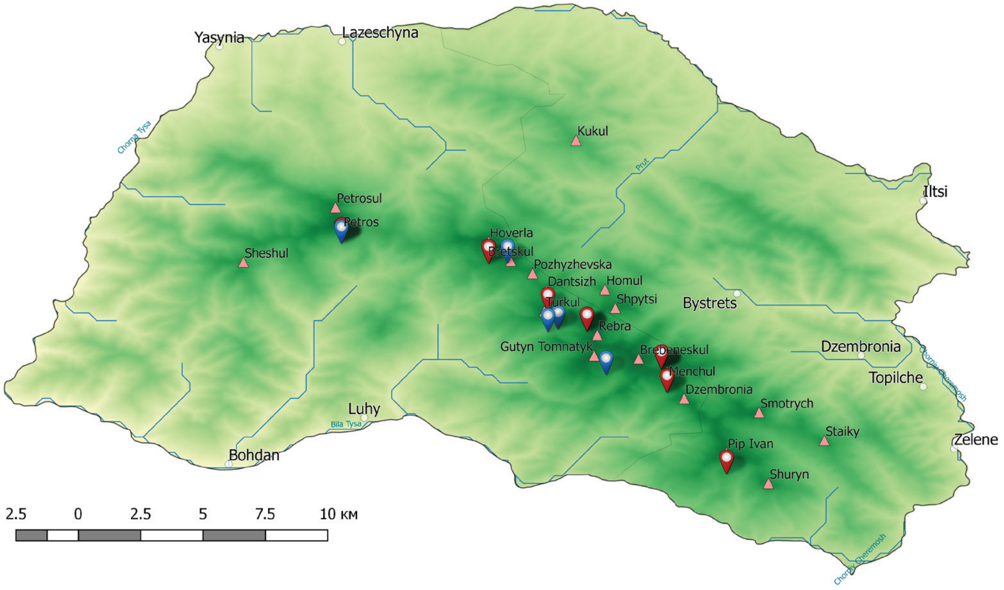

Fig. 4. Distribution of *A. firmum* in Chornohora Mts. Abbreviations correspond to Fig. 3.

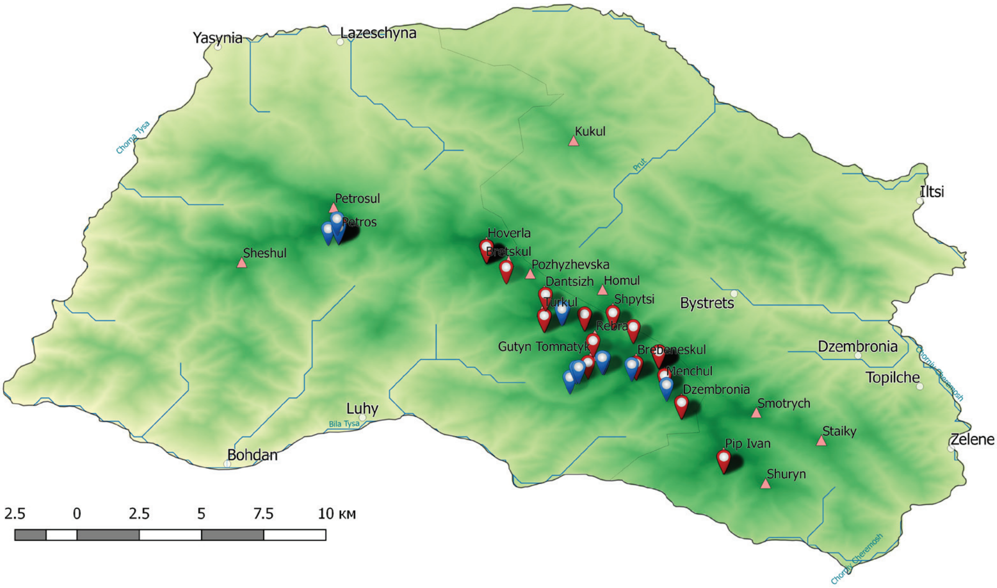

Fig. 5. Distribution of *A.* × *czarnohorense* in Chornohora Mts. Abbreviations correspond to Fig. 3.

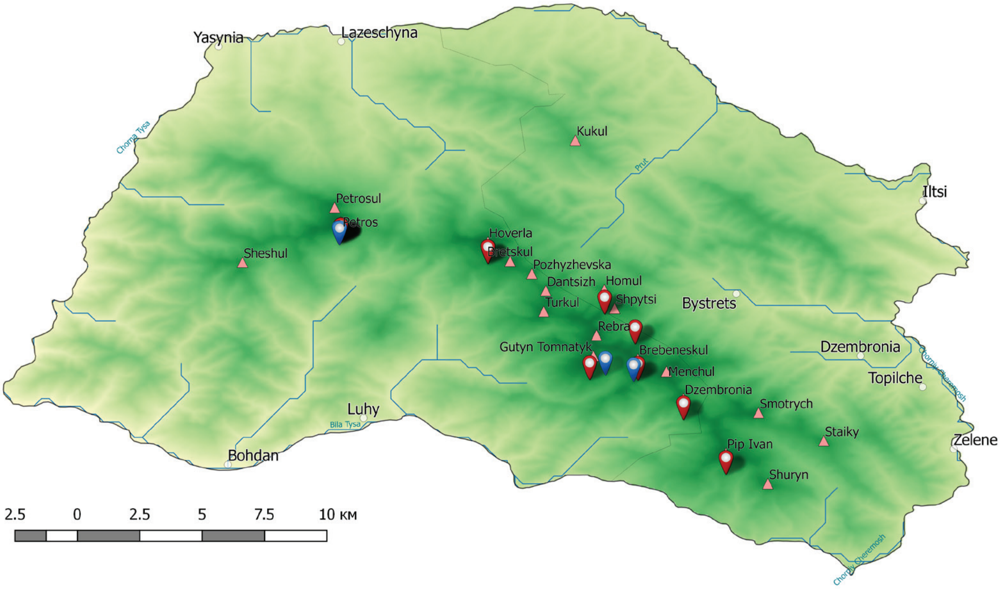

Fig. 6. Distribution of *A.* × *nanum* in Chornohora Mts. Abbreviations correspond to Fig. 3.

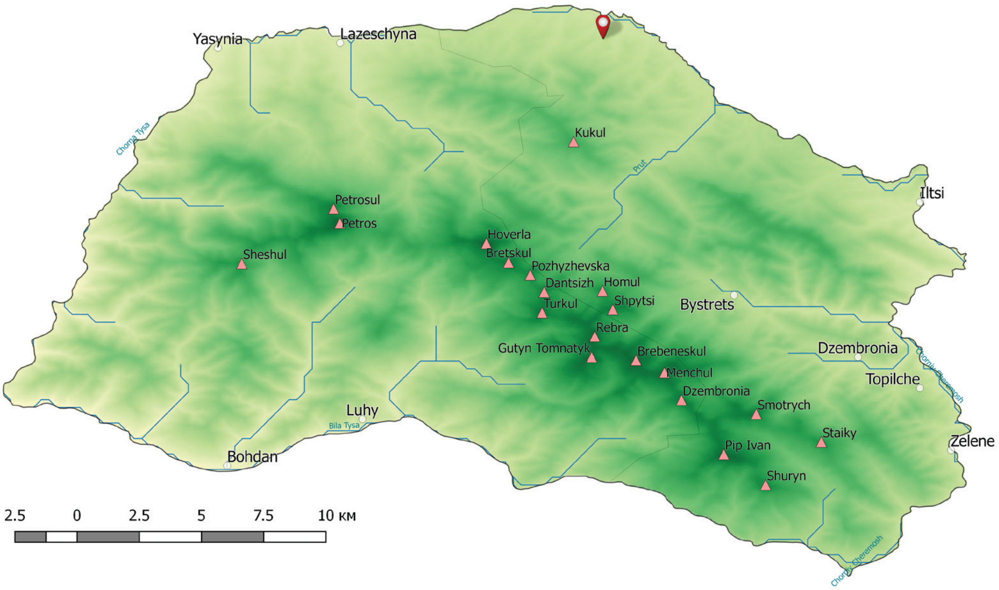

Fig. 7. Distribution of *A. variegatum* in Chornohora Mts. Abbreviations correspond to Fig. 3.

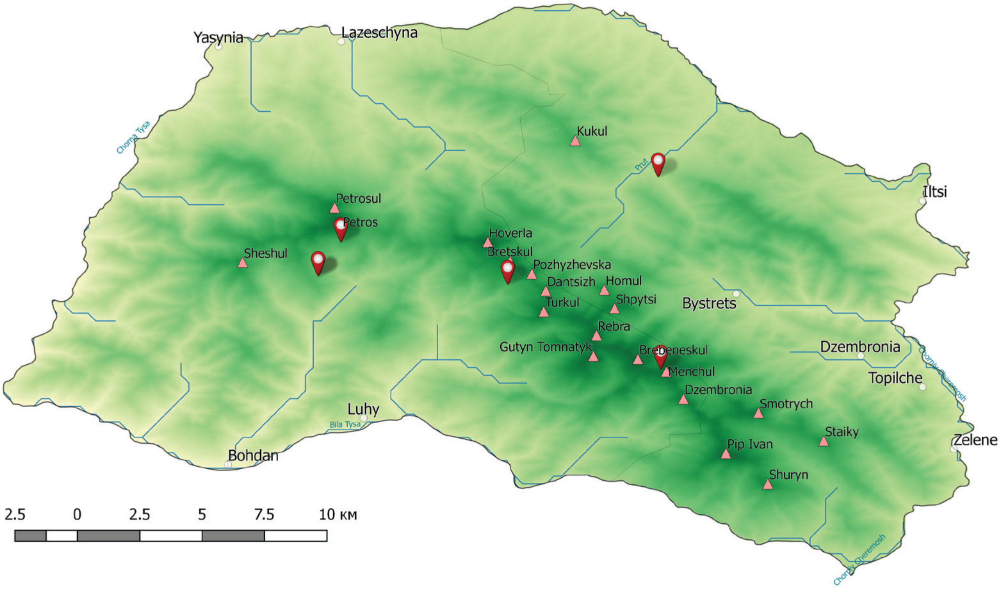

Fig. 8. Distribution of *A. lasiocarpum* in Chornohora Mts. Abbreviations correspond to Fig. 3.

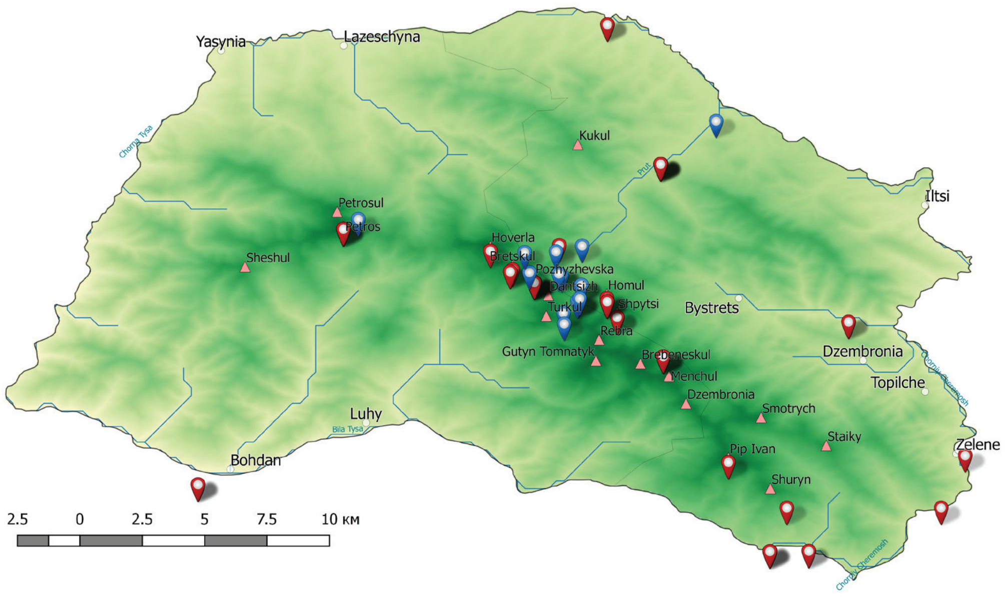

Fig. 9. Distribution of *A. degenii* in Chornohora Mts. Abbreviations correspond to Fig. 3.

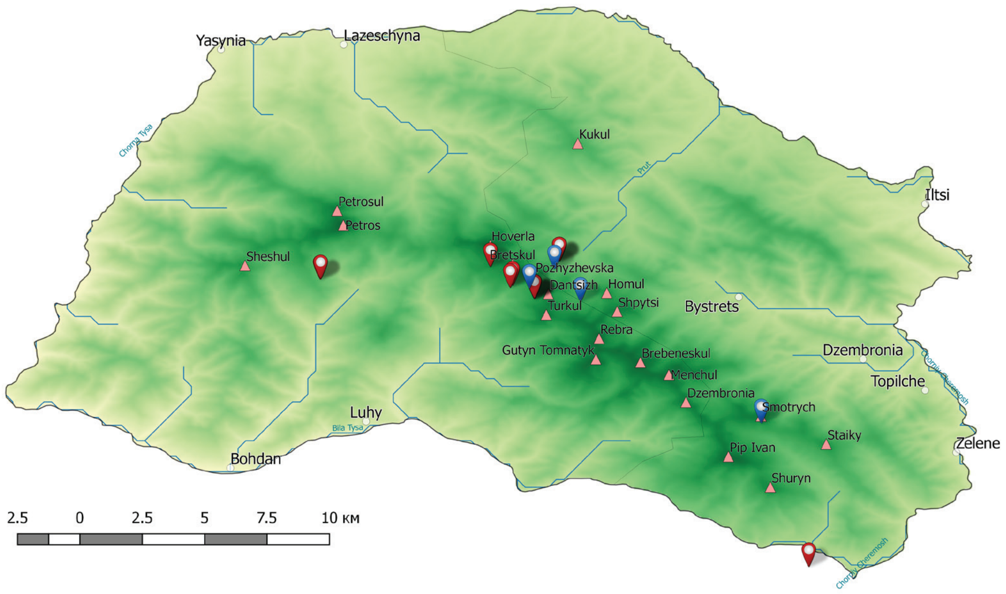

Fig. 10. Distribution of *A.* × *gayeri* in Chornohora Mts. Abbreviations correspond to Fig. 3.

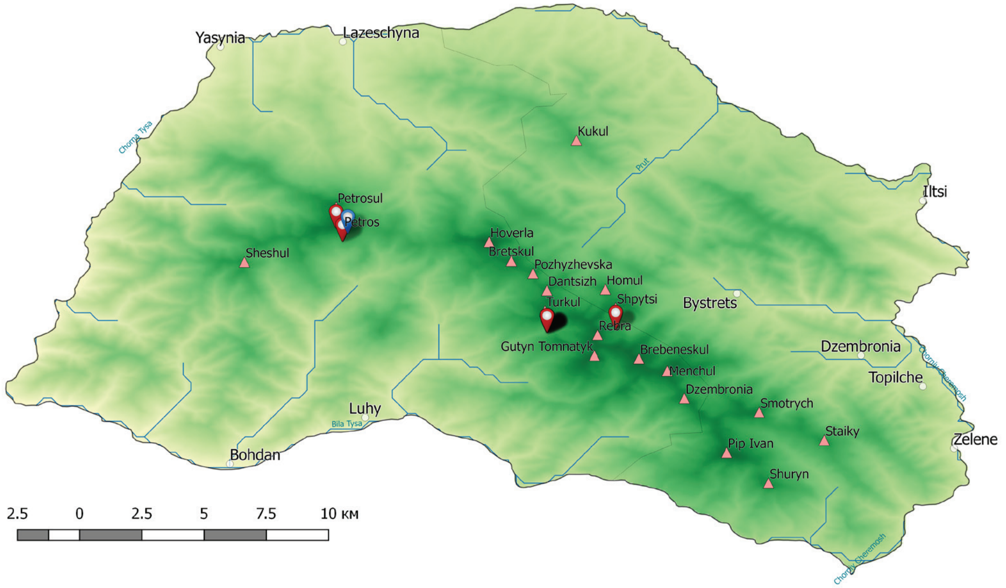

Fig. 11. Distribution of *A. anthora* in Chornohora Mts. Abbreviations correspond to Fig. 3.

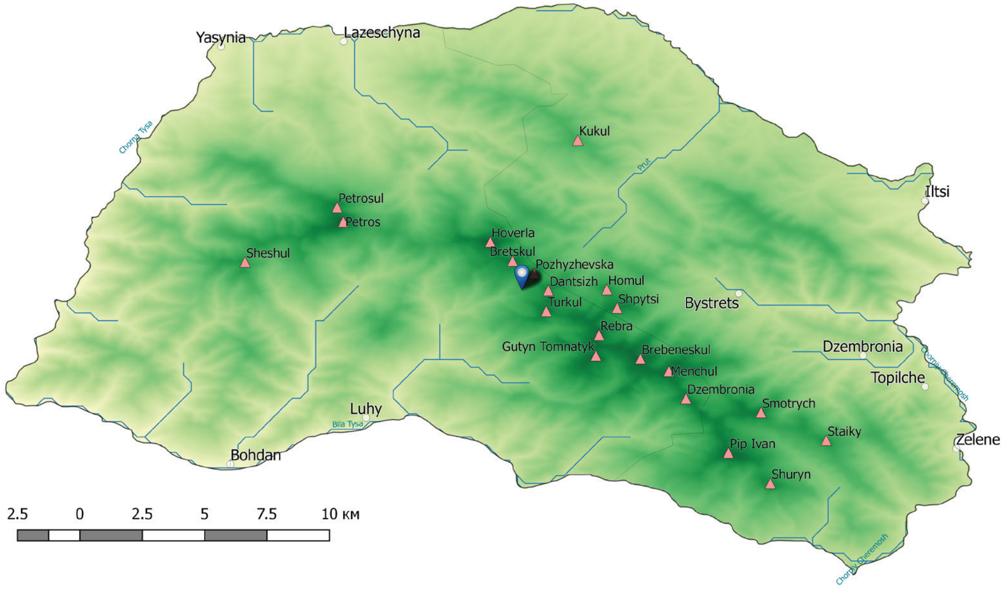

Fig. 12. Distribution of *A. lycoctonum* in Chornohora Mts. Abbreviations correspond to Fig. 3.

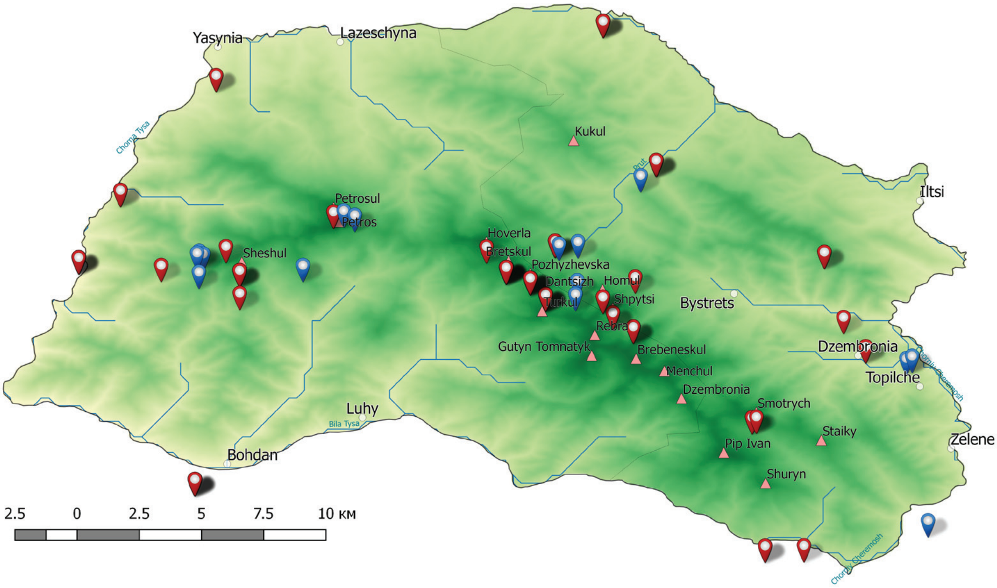

Fig. 13. Distribution of *A. moldavicum* in Chornohora Mts. Abbreviations correspond to Fig. 3.

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Appendix 1. Analyzed localities.

Location data:					
Nr	1	2	3	4	5
Description	NW slope of Petros Mt., near the summit, between stones and grasses	NE slope of Petros Mt. from the side of Petrosul Mt., stones + grasses	Rocks on E slope of Petrosul Mt., *Alnus* shrubs on steep rocks	At the foot of Petrosul Mt., rocks + shrubs	
N, °	48.171472	48.17614	48.18049	48.17815	
E, °	24.420417	024.41957	024.42319	024.42910	
Altitude, m a.s.l.	2010	1846	1724	1458	
Exposition, °	310	40	70	110	
Slope, °	15	40	80	20	
Date	22.07.2015	22.07.2015	22.07.2015	22.07.2015	
Time	13:00	14:07	15:20	16:40	
Author(s)	Novikoff A.V.	Novikoff A.V.	Novikoff A.V.	Novikoff A.V.	
Area of releve, m^2	10	10	10	10	
Fragmentation	medium	medium	high	low	
Mowing	no	no	no	no	
Pasture	no	no	no	no	
Trampling	low	no	no	no	
Succession	no	no	no	no	
Domestic animals	na	na	na	na	
Air data:					
Air t, °C	27.2	27.3	28.7	26.8	
Air relative humidity, %	43.3	40.1	43.5	46.9	
Illumination, klx	75.2	80.2	77.5	59.4	
Wind speed, m/s	8.3	7.6	3.8	2.4	
Soil data:					
Soil type (UA)	бурозем гірсько-лучний кислий альпійський слаборозвинений середньосуглинковий	бурозем гірсько-лучний кислий альпійський короткопрофільний легкосуглинковий	дерновий скелетний слаборозвинений важкосуглинковий	бурозем кислий короткопрофільний середньосуглинковий	
Soil type (EU)	Cambic Leptosols (Humic Distric)	Cambic Leptosols (Humic Distric)	Haplic Leptosols (Distric)	Leptic Cambisols (Distric Siltic)	
Soil t, °C	14.2	14.3	16.9	16.2	
Soil moisture, %	40.7	38.5	40.8	32.3	
Superficial soil moisture, %	165.12	160.21	89.01	135.21	
Soil pH	4.30	4.24	4.84	3.72	

Appendix 1. Continued.

Location data:					
Nr	6	7	8	9	10
Description	Road from Goverla Mt. to Pavlyk Mt., the lower travers, under the Petros Mt., slopes with shrubs	Road from Keveliv to high-mountain station of Lviv University, *Fagus-Acer-Picea* mixed forest	Stream in mixed forest near the road from Polonyna Vesnarka to Polonyna Kinets	Saddle between Breskul Mt. and Pozhyzhevska Mt., alpine grasslands, sampled just after the rain	Path from High-mountain Station of Institute of Ecology of Carpathians on Pozhyzhevska Mt. to Nesamovyte lake, along the stream on open place
N, °	48.15110	48.15773	48.14749	48.14704	48.14887
E, °	024.40123	024.34424	024.34522	024.51665	024.53673
Altitude, m a.s.l.	1526	1248	1243	1771	1372
Exposition, °	90	25	245	110	55
Slope, °	60	60	39	10	20
Date	22.07.2015	23.07.2015	23.07.2015	24.07.2015	25.07.2015
Time	19:50	12:40	17:25	19:05	10:55
Author(s)	Novikoff A.V.	Novikoff A.V.	Novikoff A.V.	Novikoff A.V.	Novikoff A.V.
Area of releve, m^2	10	10	10	10	10
Fragmentation	medium	high	no	no	medium
Mowing	no	no	no	no	no
Pasture	medium	low	low	no	no
Trampling	low	low	no	medium	high
Succession	low	low	low	no	medium
Domestic animals	cows, horses	cows	cows	na	na
Air data:					
Air t, °C	21.0	24.5	25.3	16.7	31.1
Air relative humidity, %	59.8	51.4	55.7	77.2	39.5
Illumination, klx	1.5	1.09	24.2	9.5	91.6
Wind speed, m/s	0	1.2	0	8.4	1.1
Soil data:					
Soil type (UA)	бурозем кислий короткопрофільний середньосуглинковий	бурозем кислий потужний сильнощебенистий середньосуглинковий	алювіальний дерновий середньосуглинковий	лучно-болотний легкоглинистий	алювіальний дерново-буроземний легкосуглинковий
Soil type (EU)	Leptic Cambisols (Distric Siltic)	Haplic Cambisols (Distric Skeletic Siltic)	Calcic Fluvisols (Calcaric Eutric Siltic)	Umbric Gleysols (Distric Clayic)	Haplic Fluvisols (Eutric Siltic)
Soil t, °C	14.7	14.7	14.4	12.9	12.1
Soil moisture, %	40.5	39.0	43.9	41.5	42.5
Superficial soil moisture, %	83.23	278.43	136.92	57.95	77.14
Soil pH	5.32	5.11	7.23	5.02	5.81

Appendix 1. Continued.

Location data:					
Nr	11	12	13	14	15
Description	Path from High-mountain Station of Institute of Ecology of Carpathians of NAS of Ukraine on Pozhyzhevska Mt. to Nesamovyte lake, along the stream in shady *Picea* forest		Lake Nesamovyte, in grasses	N slope of Turkul Mt. above the lake Nesamovyte, in grasses, sampled in low rain	Lake Brebeneskul, on wet places and along the stream, sampled after the rain
N, °	48.14292		48.12208	48.12420	48.10136
E, °	024.54886		024.53961	024.53189	024.56233
Altitude, m a.s.l.	1387		1741	1846	1783
Exposition, °	10		335	10	0
Slope, °	12		9	37	0
Date	25.07.2015		25.07.2015	26.07.2015	26.07.2015
Time	12:55		16:00	12:00	13:55
Author(s)	Novikoff A.V.		Novikoff A.V.	Novikoff A.V.	Novikoff A.V.
Area of releve, m^2	10		10	10	10
Fragmentation	medium		medium	medium	high
Mowing	no		no	no	no
Pasture	no		no	no	no
Trampling	medium		high	high	high
Succession	low		medium	no	medium
Domestic animals	na		na	na	na
Air data:					
Air t, °C	21.7		31.2	17.9	13.8
Air relative humidity, %	55.3		35.6	67.7	77.4
Illumination, klx	1.35		23.2	4.9	14.6
Wind speed, m/s	0		1.5	1.5	7.6
Soil data:					
Soil type (UA)	алювіальний дерново-буроземний легкосуглинковий		бурозем кислий короткопрофільний легкосуглинковий	бурозем гірсько-лучний кислий альпійський слаборозвинений середньосуглинковий	болотний мінеральний легкоглинистий
Soil type (EU)	Haplic Fluvisols (Calcaric Eutric Siltic)		Leptic Cambisols (Distric Siltic)	Cambic Leptosols (Humic Distric)	Mollic Gleysols (Humic Distric Clayic)
Soil t, °C	13.7		13.0	14.2	12.3
Soil moisture, %	41.1		40.1	36.3	40.5
Superficial soil moisture, %	115.84		65.95	37.27	410.20
Soil pH	6.13		3.96	3.50	5.93

Appendix 1. Continued.

Location data:				
Nr	16	17 18	19	20 21
Description	ES slope of Gutyn-Tomnatyk Mt., inside the *Juniperus* shrubs separately located on alpine grassland, highly fragmented population	Path from High-mountain Station of Institute of Ecology of Carpathians on Pozhyzhevska Mt. to Nesamovyte lake, along the open stream in *Picea* forest	Road from Zarosliak to Station of Institute of Ecology of Carpathians, open wet places along the road in Picea forest	Road from Vorokhta to Zarosliak, open stream in *Picea* forest
N, °	48.09629	48.13560	48.16082	48.16387
E, °	024.54967	024.54792	024.53525	024.54923
Altitude, m a.s.l.	1915	1458	1310	1179
Exposition, °	11	335	50	52
Slope, °	25	20	10	2
Date	26.07.2015	26.07.2015	27.07.2015	27.07.2015
Time	16:00	18:55	11:25	14:00
Author(s)	Novikoff A.V.	Novikoff A.V.	Novikoff A.V.	Novikoff A.V.
Area of releve, m^2	10	10	10	10
Fragmentation	high	no	medium	no
Mowing	no	no	no	no
Pasture	no	no	no	no
Trampling	no	low	high	low
Succession	no	no	medium	low
Domestic animals	na	na	na	na
Air data:				
Air t, °C	22.6	17.9	14.4	23.7
Air relative humidity, %	55.4	66.9	78.8	64.1
Illumination, klx	33.4	1.43	9.8	4.6
Wind speed, m/s	8.6	0	0.9	1.3
Soil data:				
Soil type (UA)	бурозем гірсько-лучний кислий альпійський слаборозвинений середньосуглинковий	алювіальний дерново-буроземний легкосуглинковий	алювіальний дерново-буроземний легкосуглинковий	алювіальний дерново-буроземний легкосуглинковий
Soil type (EU)	Cambic Leptosols (Humic Distric)	Haplic Fluvisols (Calcaric Eutric Siltic)	Haplic Fluvisols (Calcaric Eutric Siltic)	Haplic Fluvisols (Calcaric Eutric Siltic)
Soil t, °C	10.9	12.5	11.7	12.3
Soil moisture, %	39.8	39.8	40.5	41.1
Superficial soil moisture, %	180.90	120.03	55.66	293.81
Soil pH	3.70	5.42	4.90	4.52

Appendix 1. Continued.

Location data:						
Nr	22	23	24 stones	24 grasslands	25	26
Description	N slope of Goverla Mt., in alpine grasslands on open place	Waterfall Prutskiy under Goverla Mt., in grasses along the stream	Mt. Brebeneskul, just near the summit on alpine grasslands and in depressions between stones		Near the summit of Menchul Mt., in grasses between stones	Road from Pogorilets to Zelene (Yavirnyk) village, on the steep slopes along the road, on the edge of mixed forest
N, °	48.16132	48.16039	48.09775		48.08686	48.01366
E, °	024.51023	024.51841	024.57818		024.59693	024.73768
Altitude, m a.s.l.	1793	1459	1978		1882	822
Exposition, °	70	40	325		300	170
Slope, °	32	20	18		32	60
Date	27.07.2015	27.07.2015	28.07.2015		28.07.2015	29.07.2015
Time	16:30	17:15	14:30		16:00	8:10
Author(s)	Novikoff A.V.	Novikoff A.V.	Novikoff A.V.		Novikoff A.V.	Novikoff A.V.
Area of releve, m^2	10	10	10		10	10
Fragmentation	no	no	low		no	high
Mowing	no	no	no		no	no
Pasture	no	no	no		no	medium
Trampling	no	low	low		low	high
Succession	no	no	no		no	high
Domestic animals	na	na	na		na	cows, horses
Air data:						
Air t, °C	15.6	17.8	14.2		11.0	16.1
Air relative humidity, %	64.0	71.9	62.7		69.5	76.0
Illumination, klx	21.1	16.7	101.2		11.9	2.0
Wind speed, m/s	8.1	0	1.7		9.8	0
Soil data:						
Soil type (UA)	бурозем кислий субальпійський короткопрофільний легкосуглинковий	алювіальний дерново-буроземний легкосуглинковий	дерновий скелетний слаборозвинений легкоглинистий	бурозем гірсько-лучний кислий альпійський короткопрофільний важкосуглинковий	бурозем гірсько-лучний кислий альпійський короткопрофільний легкосуглинковий	алювіальний дерновий легкосуглинковий
Soil type (EU)	Leptic Cambisols (Distric Siltic)	Haplic Fluvisols (Calcaric Eutric Siltic)	Haplic Leptosols (Distric)	Leptic Cambisols (Distric Siltic)	Leptic Cambisols (Distric Siltic)	Calcic Fluvisols (Calcaric Eutric Siltic)
Soil t, °C	17.0	14.3	9.5	9.7	10.7	15.2
Soil moisture, %	40.3	41.3	39.8	40.9	40.5	41.0
Superficial soil moisture, %	17.89	113.46	15.81	100.85	38.04	26.26
Soil pH	5.06	5.66	3.93	5.04	4.20	7.40

Appendix 2. Population data. Numbers of entries correspond to App. 1.

Nr	Taxa analyzed in July 2015	Taxa totally observed	Postgenerative plants, pcs./m^2	Generative plants, pcs./m^2	Pregenerative plants, pcs./m^2	Density, pcs./m^2	Total quantity, pcs.	Condition, 1-4	Area of population, m^2
1	*A.* × *czarnohorense*	*A.* × *czarnohorense*, *A.* × *nanum*, *A. firmum* ssp. *fissurae*	0	3	2	5	~100	3	>500
2	*A.* × *czarnohorense*	*A.* × *czarnohorense*	1	3	3	6	<50	3	~500
3	*A. moldavicum* ssp. *moldavicum*	*A. moldavicum* ssp. *moldavicum*	0	1	2	3	<10	2	~20
4	*A. moldavicum* ssp. *hosteanum*	*A. moldavicum* ssp. *hosteanum*, *A. degenii* ssp. *degenii* f. *craciunelense*, *A. bucovinense* f. *orthotricha*, *A. anthora*	0	2	3	3	8	2	~20
5	*A. degenii* ssp. *degenii* f. *craciunelense*	*A. moldavicum* ssp. *hosteanum*, *A. degenii* ssp. *degenii* f. *craciunelense*, *A. bucovinense* f. *orthotricha*, *A. anthora*	0	3	3	3	9	2	~20
6	*A. moldavicum* ssp. *hosteanum*, *A. moldavicum* ssp. *moldavicum*	*A. moldavicum* ssp. *hosteanum*, *A. moldavicum* ssp. *moldavicum*	1	5	5	11	~20	4	~200
7	*A. moldavicum* ssp. *hosteanum*	*A. moldavicum* ssp. *hosteanum*	1	0	0	0	1	1	~10
8	*A. moldavicum* ssp. *hosteanum*	*A. moldavicum* ssp. *hosteanum*	0	2	3	5	5	2	~20
9	*A. bucovinense* f. *orthotricha*	*A. bucovinense* f. *orthotricha*	2	14	4	20	>50	4	>500
10	*A. degenii ssp. degenii f. degenii*	*A. degenii* ssp. *degenii* f. *degenii*, *A. degenii* ssp. *degenii* var. *intermedium*	3	10	12	25	>200	4	~250
11	*A. moldavicum* ssp. *hosteanum*	*A. moldavicum* ssp. *hosteanum*, *A. degenii* ssp. *degenii* var. *intermedium*, *A.* × *gayeri*	0	1	3	4	~10	4	~100
12	*A. degenii* ssp. *degenii* var. *intermedium*	*A. moldavicum* ssp. *hosteanum*, *A. degenii* ssp. *degenii* var. *intermedium*, *A.* × *gayeri*	0	10	5	15	>40	4	~100
13	*A. degenii* ssp. *degenii* f. *degenii*	*A. degenii* ssp. *degenii* f. *degenii*	1	9	20	30	~50	2	<30
14	*A. firmum* ssp. *fissurae*	*A. firmum* ssp. *fissurae*	1	2	4	7	>300	4	~500
15	*A.* × *czarnohorense*	*A.* × *czarnohorense*, *A.* ×*nanum*, *A. firmum ssp. fissurae*	8	10	12	30	>500	4	~400

Appendix 2. Continued. Numbers of entries correspond to App. 1.

Nr	Taxa analyzed in July 2015	Taxa totally observed	Postgenerative plants, pcs./m^2	Generative plants, pcs./m^2	Pregenerative plants, pcs./m^2	Density, pcs./m^2	Total quantity, pcs.	Condition, 1-4	Area of population, m^2
16	*A.* × *czarnohorense*	*A.* × *czarnohorense*	2	2	2	6	~50	3	>1000
17	*A. degenii* ssp. *degenii* f. *craciunelense*	*A. degenii* ssp. *degenii* f. *craciunelense, A. degenii* ssp. *degenii* var. *intermedium, A. moldavicum ssp. hosteanum*	0	4	8	12	>50	4	~60
18	*A. moldavicum* ssp. *hosteanum*	*A. degenii* ssp. *degenii* f. *craciunelense, A. degenii* ssp. *degenii* var. *intermedium, A. moldavicum ssp. hosteanum*	1	2	3	6	~10	3	~60
19	*A. degenii* ssp. *degenii* var. *intermedium*	*A. degenii* ssp. *degenii* var. *intermedium, A.* ×*gayeri*	0	4	5	9	~50	3	~100
20	*A. moldavicum* (sterile mutant)	*A. moldavicum* (sterile mutant), *A. degenii* ssp. *degenii* f. *degenii*	1	1	1	3	<5	1	~10
21	*A. degenii* ssp. *degenii* f. *degenii*	*A. moldavicum* (sterile mutant), *A. degenii* ssp. *degenii* f. *degenii*	1	7	12	20	>500	4	>500
22	*A. firmum* ssp. *fissurae*	*A. firmum* ssp. *fissurae*	0	1	0	1	1	1	1 (?)
23	*A. degenii* ssp. *degenii* f. *degenii*	*A. degenii* ssp. *degenii* f. *degenii*	1	8	3	12	>400	4	>400
24 s	*A.* × *czarnohorense, A.* × *nanum*	*A.* × *czarnohorense, A.* × *nanum*	0	2	5	7	>1000	4	~1000
24 g	*A.* × *czarnohorense, A.* × *nanum*	*A.* × *czarnohorense, A.* × *nanum*	6	14	10	30	>1000	4	~1000
25	*A.* × *czarnohorense*	*A.* × *czarnohorense*	0	6	10	16	>200	4	~500
26	*A. moldavicum* ssp. *moldavicum*	*A. moldavicum* ssp. *moldavicum*	1	2	2	5	<10	2	~50

Appendix 3. Releves. Numbers of entries correspond to App. 1.

Nr	1	2	3	4	5	6	7	8	9	10	11	12
Community	*Caricetum sempervirentis*	*Caricetum sempervirentis*	*Pulmonario-Duschekietum viridis*	*Juniperetum sibiricae*	*Juniperetum sibiricae*	*Pulmonario-Duschekietum viridis*	-	-	*Poo-Deschampsietum*	*Vaccinio myrtilli-Pinetum mughi*	*Calthion*	*Calthion*
Mosses & lichens, %	5	10	5	3	3	5	8	5	2	10	20	20
Herbs, %	70	70	30	40	40	20	40	60	98	50	60	60
maximal height, cm	70	60	50	70	70	120	100	140	80	140	120	120
average height, cm	25	25	20	30	30	60	50	20	50	60	30	30
Shrubs, %	2	5	40	25	25	40	20	10	0	20	5	5
maximal height, cm	20	30	200	160	160	180	170	320	0	200	300	300
average height, cm	10	20	60	100	100	140	120	250	0	160	60	60
Trees, %	0	0	0	2	2	20	0	10	0	0	0	0
maximal height, cm	0	0	0	500	500	400	0	500	0	0	0	0
average height, cm	0	0	0	350	350	250	0	250	0	0	0	0
Uncovered soil, %	0	0	5	0	0	10	30	12	0	0	5	5
Rocks and stones, %	25	15	20	30	30	5	2	3	0	20	10	10
Taxa and projective covering:												
Achillea carpatica				2m	2m				1			
Aconitum anthora				+	+							
Aconitum bucovinense f. *orthotricha*				r	r				1			
Aconitum × *czarnohorense*	r	r										
Aconitum degenii ssp. *degenii* f. *craciunelense*				r	r							
Aconitum degenii ssp. *degenii* f. *degenii*										1		
Aconitum degenii ssp. *degenii* var. *intermedium*										1	1	1
Aconitum firmum ssp. *fissurae*	r											
Aconitum × *gayeri*											+	+
Aconitum moldavicum ssp. *hosteanum*				r	r	+		r			+	+
Aconitum moldavicum ssp. *moldavicum*			r			r	r					
Aconitum ×*nanum*	r											
Adenostyles alliariae												
Agrostis tenuis				2a								
Alchemilla sp.				2a	2a					2b		

13	14	15	16	17	18	19	20	21	22	23	24 s	24 g	25	26
Phleo alpini-Deschampsietum caespitosae	*Poo-Deschampsietum*	*Aconitetum firmi / Ranunculo platanifolii-Adenostyletum alliariae*	*Primulo-Caricetum curvulae*	*Calthetum laetae*	*Calthetum laetae*	*Calthion*	*Ranunculo platanifolii-Adenostyletum alliariae*	*Ranunculo platanifolii-Adenostyletum alliariae*	*Poo-Deschampsietum / Juniperetum sibiricae*	*Ranunculo platanifolii-Adenostyletum alliariae*	-	*Poo-Deschampsietum*	*Poo-Deschampsietum*	-
5	5	0	10	30	30	5	20	20	0	10	20	0	0	0
80	80	90	10	40	40	60	70	70	80	85	10	90	70	60
80	70	80	40	150	150	120	190	190	70	80	60	60	80	140
30	30	40	30	70	70	30	60	60	60	40	20	10	30	50
0	5	10	80	10	10	20	5	5	18	5	0	0	10	10
0	40	60	40	80	80	140	140	140	100	200	0	0	90	200
0	20	40	30	60	60	80	20	20	80	140	0	0	40	160
0	0	0	0	0	0	15	5	5	0	0	0	0	0	0
0	0	0	0	0	0	800	300	300	0	0	0	0	0	0
0	0	0	0	0	0	500	200	200	0	0	0	0	0	0
0	0	0	0	5	5	0	0	0	0	0	0	0	0	13
15	10	0	0	15	15	0	0	0	2	2	70	10	20	2
										1				
		1	1								r	2a	+	
				1	1		2m	2m						
2b										2a				
				+	+	1								
	2m	r							r					
						r								
				+	+									
							r	r						r
		1								4	r	+		
		2m					3	3						
						3								

Appendix 3. Continued. Numbers of entries correspond to App. 1.

Nr	1	2	3	4	5	6	7	8	9	10	11	12
Alchemilla subcrenata												
Allium ursinum								1				
Alnus viridis			5	2m	2m	5				2b		
Anthoxanthum alpinum		2b		2a					2m			
Anthoxanthum odoratum										2m		
Arcticum lappa												
Aruncus sylvestris							2a					
Astrantia major										1		
Athyrium filix-femina				1		2a	2b	+		2a	2a	
Atrichum undulatum							2a					
Avenula versicolor	2a		2b			+						
Calamagrostis villosa							2b					
Calliergonella cuspidata							3					
Caltha palustris ssp. *laeta*												
Campanula cervicaria												
Campanula kladniana												
Campanula glomerata				2a	2a							
Campanula patula ssp. *abietina*										r	1	
Campanula polymorpha ssp. *rotundifolia*	2b	3	2b									
Carduus bicolorifolius										2a		
Cardamine opizii												
Carex atrata												
Carex curvula												
Carex echinata												
Carex rostrata												
Carex sempervirens	2b	2m										
Carex sylvatica								1				
Centaurea phrygia ssp. *carpatica*						2b						
Centraria islandica	1								2b			
Cerastium fontanum									+			
Chaerophyllum hirsutum											4	
Cimicifuga europaea								2a		2m		
Cirsium vulgare												
Cirsium waldsteinii						2m						
Clematis alpina			r									
Crepis paludosa								2m			2b	
Cystopteris fragilis								r				
Dactylis glomerata												
Daphne mezereum				1	1							
Deschampsia caespitosa	2m	4	1	3				1	5	1	r	

13	14	15	16	17	18	19	20	21	22	23	24 s	24 g	25	26
				1	1					3				
										2m				
		1												
														1
+	+			2a		+	2a			2m			+	
		2a		2b		3	+					r		
														2b
										r				
2m														
	2a		2m						2m		r	2m	2a	
							1							
		3												
		+												
			2m											
						2a								
				+										
	2m		1											
						1								1
			1											
				2a		1	2m							
														+
				3		2a	1			2m				
				1		2b				r				
														+
														r
4	4		1	2b		2a	2m		4	2a		5	5	

Appendix 3. Continued. Numbers of entries correspond to App. 1.

Nr	1	2	3	4	5	6	7	8	9	10	11	12
Dicranella varia												
Dicranum scoparium												
Dicranum sp.											2b	
Doronicum austriacum										2m	1	
Doronicum carpaticum												
Empetrum nigrum												
Epilobium alpestre										2a		
Epilobium alsinifolium												
Epilobium angustifolium								+				
Epilobium montanum						2a						
Euphorbia amygdaloides												
Equisetum sylvaticum												
Fagus sylvatica								2a				
Festuca airoides	3		2b						2b			
Festuca picturata												
Festuca rubra									2b	1		
Festuca supina												
Filipendula ulmaria												
Fragaria vesca								2b				
Galeopsis speciosa											3	
Galium bellatulum			+									
Galium carpaticum						1						
Gentiana acaulis			1									
Gentiana asclepiadea				1	1	1	2m					
Gentiana punctata												
Geranium alpestre		1							r			
Geranium sanguineum								1				
Geum montanum	1	1	+									
Geum urbanum												
Grimmia sp.			2b									
Hieracium alpinum ssp. *alpinum*	2b	+	1						1			
Hieracium pilosella												
Hieracium sp.			1							1		
Hieracium umbrosum												
Homogyne alpina	+			+	+				+			
Huperzia selago		+										
Hygroamblystegium varium								1				
Hylocomium splendens												
Hypericum maculatum										2b		
Hypericum richeri	1	2b		+		2m			+	2b		
Hypericum perforatum												

13	14	15	16	17	18	19	20	21	22	23	24 s	24 g	25	26
2a														
							4							
							2m							
		+								1				
			3											
		2a												
				1	1									
							1	1						
							r							+
						+								1
														+
		4	3							2a		3		
	2a	2a												
3											2m		1	
			2b						3	+			1	
				2a			2a							
							1	1						+
														+
									r					
						1								
		1												
									r	r				
2b									1			2m	1	
							+							1
1	2b		2a									1	+	
				r										
2b	+		+				3	1	r					
							1	1			r			
	+													
							2a							
1	2b									1		r	1	
													1	

Appendix 3. Continued. Numbers of entries correspond to App. 1.

Nr	1	2	3	4	5	6	7	8	9	10	11	12
Hypochoeris uniflora		+										
Juncus alpino-articulatus ssp. *fuscoater*												
Juncus effusus												
Juncus trifidus	2m	2a	1									
Juniperus communis	+	1	3	3	4							
Laserpitium krapfii												
Leontodon croceus												
Leucanthemum rotundifolia											2m	
Leucanthemum waldsteinii				1		1	r					
Leucanthemum vulgare										r		
Ligusticum muttelina									r			
Luzula alpinopilosa	1											
Luzula luzuloides									2a			
Luzula sylvatica												
Marchantia polymorpha							2b	2a				
Melica nutans												
Myosotis alpestris												
Myosotis caespitosa									1	+		
Myosotis strigulosa											4	
Myosoton aquaticum									1			
Nardus stricta				2m	2m							
Origanum vulgare												
Oxalis acetosella							+				2b	2b
Pedicularis verticillata												
Petasites albus										2a	1	1
Petasites kablikianus								1			2b	2b
Phleum alpinum				3						r		
Phyteuma vagneri		1	1									
Picea abies								r			1	1
Pinus mugo										3		
Plagiomnium rostratum										2a		
Poa alpina				2b								
Poa chaixii				3					3			
Poa deylii	1		2a									
Poa media												
Poa nemoralis												
Polygonum bistorta										1		
Polypodium vulgare												
Polytrichum formosum									2a	2a		
Potentilla aurea		1							+			
Potentilla erecta	2m											

13	14	15	16	17	18	19	20	21	22	23	24 s	24 g	25	26
						3								
							1							
2a	4		4						1		+	+	2b	
	2a	2m	5						3				1	
2a														
		1												
		r		2m		2b				1				
							2a							1
		1												
		r							1				2m	
	2m													
						2a	4							
														+
		1												
				2b		2m	3			+				
1		1												
														2m
				2b	2b	+	2b	2b						
		2m												
				5	5	4								
2a										1				
	2a													
				1	1	+	+	2a					r	
						+	2a							
											2m			
1	2a												2m	
									+					
												1		
														+
										2m				
							r							
				3	3	2b	4	4		1	2a			
2m			+						+			+	+	

Appendix 3. Continued. Numbers of entries correspond to App. 1.

Nr	1	2	3	4	5	6	7	8	9	10	11	12
Prenanthes purpurea												
Primula elatior ssp. *poloninensis*								+				
Prunella vulgaris				1		1				3		
Pulmonaria mollis												
Pulsatilla alba		3	1									
Ranunculus acris							2m					
Ranunculus illyricus									1			
Ranunculus lanuginosus								1				
Ranunculus platanifolius												
Ranunculus repens											3	
Rhodiola rosea		2m										
Rhododendron myrtifolium		2m										
Rhytidiadelphus squarrosus										3		
Rhytidiadelphus triquetrus			2a									
Rosa pendulina												
Rumex alpestris										r		
Rumex carpaticus											r	
Rubus idaeus				4	4	2a	3			1	1	1
Rubus sp.										1		
Salix silesiaca												
Salvia glutinosa												
Saxifraga paniculata	+	+	+									
Schistidium sp.		1										
Scrophularia scopolii						1						
Sedum carpaticum				1		1						
Senecio carpaticus												
Senecio nemorensis						2b	1				4	
Sesleria bielzii	2b	2a	3									
Silene vulgaris ssp. *carpatica*												
Silene dioica						+						
Soldanella marmarossiensis												
Solidago virgaurea ssp. *alpestris*		+							r	+		
Sphagnum sp.												
Spiraea ulmifolia				2a								
Stellaria graminea										2m		
Stellaria nemorum											2b	
Streptopus amplexifolius											r	r
Symphytum cordatum							1					
Telekia speciosa											2m	
Thalictrum aquilegiifolium				1			2m	2b		+		
Thymus alpestris	2a	2a	2m	1	1					2a		

13	14	15	16	17	18	19	20	21	22	23	24 s	24 g	25	26
							r							
						2m	2b							1
												2a		
	+		+										1	
							r			1				
										r				
	1		4										1	
														1
						+	1	1						1
							1	1						
		3				2m								
														2a
												r		
				+										
		1	2b								+	3		
	+								1					
+	1		2a						1		r	+	+	
1	3	+					1		1	1		2		r
				2a										
							r							
													3	
								1				1		

Appendix 3. Continued. Numbers of entries correspond to App. 1.

Nr	1	2	3	4	5	6	7	8	9	10	11	12
Trollius europaeus										2m		
Torilis japonica												
Trifolium repens				+								
Urtica dioca						+		+			r	r
Vaccinium myrtillus		1	2a	2m	2m					+		
Vaccinium vitis-ideae			2a									
Vaccinium uliginosum	2a		4									
Valeriana tripteris								4				
Valeriana sambucifolia										2a		
Veratrum album		1				1	+			+		
Veronica chamaedrys												
Veronica officinalis										2m		
Veronica urticifolia							3					
Viburnum opulus							1					
Vicia cracca												
Viola biflora											4	
Viola declinata			1	+					+			

13	14	15	16	17	18	19	20	21	22	23	24 s	24 g	25	26
		2b												
														1
														+
	1		2b	4	4		2b	2b	1				+	
			1						1					
1		r					r	r						
														+
														2m
						3								
												1	1	

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DEVELOPMENT, ANATOMY, AND GENETIC CONTROL OF SOME TERATOLOGICAL PHENOTYPES OF RANUNCULACEAE FLOWERS

Florian Jabbour [1]*, Felipe Espinosa [1], Thierry Deroin [1], Domenica Manicacci [2],
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Key words: Ranunculaceae, evolution, flower, morpho-anatomy, phylogeny, teratology

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Teratological organisms originate from developmental anomalies, and exhibit structures and a body organization that deviate from the species standard. These monsters give essential clues about the formation and evolutionary significance of the wild-type groundplan. We focus on flower terata, which can be affected in their sterile and/or fertile organs, with special emphasis on the Ranunculaceae. The diversity of perianth shapes and organizations in flowers of this family is huge, and is even increased when anomalies occur during organo- and/or morphogenesis.

To begin with, we synthesize the observations and research conducted on the Ranunculacean floral terata, following the most recent phylogenetic framework published in 2016 by our team.

Then, we report results regarding the morphology of developing meristems, the anatomy of buds, and the genetic control of selected teratological phenotypes of Ranunculaceae flowers. We focus on species and horticultural varieties belonging to the genera *Aquilegia, Delphinium*, and *Nigella*. Wild-type flowers of these species are actinomorphic (*Aquilegia, Nigella*) or zygomorphic (*Delphinium*), spurred (*Aquilegia, Delphinium*) or with pocket-like petals (*Nigella*).

Last, we discuss the evolutionary potential of such teratological phenotypes when they occur in the wild.

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PERIANTH EVOLUTION IN RANUNCULACEAE: ARE PETALS ANCESTRAL IN THE FAMILY?

Sophie Nadot [1*], Hervé Sauquet [1], Catherine Damerval [2], Florian Jabbour [3], Boris Domenech [4]

Key words: Ranunculaceae, evolution, nectaries, perianth, petals, phylogeny

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Progress has been made recently towards the elucidation of phylogenetic relationships among subfamilies and tribes of the Ranunculaceae – the most recent hypothesis was published in 2016 by our team. Although relationships among the 10 tribes of the subfamily Ranunculoideae remain incompletely supported, this hypothesis provides an interesting framework to address the key issue of the ancestral vs. derived nature of a differentiated perianth within the family, and at the level of Ranunculales as a whole. Here, we present ancestral state reconstructions for several perianth characters, such as differentiation into sepals and petals, shape of petals, presence/absence of nectaries, and petaloid or sepaloid aspect of sepals. Characters were scored using the PROTEUS database and optimized on the most recent phylogeny of Ranunculaceae using parsimony and maximum likelihood methods. The results are discussed with regard to recent evo-devo studies focused on identifying genes involved in floral organs identity (the so-called ABC model) in Ranunculales.

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MODERN THEORETICAL AND TECHNICAL APPROACHES IN PLANT MORPHOLOGY

Jürg Schönenberger, Marion Chartier, Yannick Staedler

Key words: Ericales, floral structure, floral evolution, micro tomography, morphospace analysis, plant morphology

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Morphology is deeply rooted in organismal biology, which in recent years has gone through a steady decline in interest both at research institutions and funding agencies. In parallel with this development, morphology as a discipline has been marginalized and nowadays many think of it as just a classical and largely obsolete field of research. However, this is far from the truth. Thanks to modern theoretical concepts and novel technical applications, plant morphology has much to contribute to modern botanical and evolutionary research.

In our presentation, we will first outline the application of High Resolution X-Ray Computed Tomography (HRXCT) to the study of plant structure. The ideal way to describe the morphological phenotype of a given organism is to build a three dimensional (3D) model, which may then be interpreted with respect to other types of data, e.g., metabolite content or functional groups of pollinators. We have developed simple but efficient lab protocols using contrasting agents such as phosphotungstate and bismuth tartrate that allow for the streamlined acquisition of high resolution phenotypic data and 3D-representations even of soft plant tissues such as floral organs, ovules, and meristematic tissues. To illustrate this, we will outline selected ongoing studies in comparative plant science that make use of high resolution tomography.

In the second part of our talk, we will present a project on the floral morphospace. A striking feature of morphological variation is that due to developmental, functional, and phylogenetic constraints, not all theoretically possible architectures have been explored during evolution. A modern approach to studying the evolution of realized forms among possible ones is to construct morphospaces, i.e. theoretical, mathematical spaces describing and relating organismal phenotypes. Although widely applied in zoology, morphospace analyses and related approaches have so far been largely disregarded in botany, with notable exceptions in the field of pollination biology. Here, we use a morphospace approach to describe and quantify the morphological diversity (disparity) of flowers in the asterid order Ericales. To do so, we have built a dataset containing 37 floral characters for more than 380 species (275 genera) representative of the entire order. We have used non-parametric representations and statistics methods based on distance matrices to build and analyze a morphospace, in which we compare the relative positions of the different ericalean families. We quantify and interpret the disparity among these groups in the light of their taxonomic diversity, their evolutionary history, and their ecology. In addition, we analyze patterns of disparity between sterile, male, and female floral organs.

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MORPHOLOGICAL DEVELOPMENT OF PETALS IN RANUNCULACEAE

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Key words: Ranunculaceae, petal, morphological development

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The petals, or the honey-leaves, are of great divergence in morphology in Ranunculaceae, i. e., tubular, bilabial, cup-shaped, flat, concaved or scaled at the base, with or without spur or succate. The previous observations showed that although the petals differ in mature morphology, they showed great similarity in the early development stage. The petal primordia are all hemispherical, rounded and much smaller than the sepal primordia, a relatively long plastochron exists between the last sepal and the first petal and differentiate into a blade and a short stalk. Thus, we assumed that the different morphology of the mature petals might be due to the morphological repatterning of petals in the development. To prove the hypothesis, the morphological development of the petals from 22 species from 20 genera, recovering all ten petalous clades and the major morphological types, in Ranunculaceae was observed by scanning electron microscope (SEM).

The young petal undergoes the following developmental stages to the mature petal after it differentiates into blade and stalk. In the first stage, a depression appears at the base of the blade and the nectary tissue will appear in the depression in the later development. In the second stage, two bulges appear at the base of the depression that makes the petal bilabial and the bulges will be the upper lip of the petal and thus the blade will be the lower lip. In the third stage, two bulges become larger and fuse with one another at first and then fuse with the margins of the blade in each side, or each of the bulges fuses with the margin of the blade at first and then fuses with one another, or the bulges stop further growth and the depression deepened to form the succate or the spur. In the fourth stage, the lips, the two fused sides and the stalk growth in different speed.

The divergence of development of different petals happens mainly in the third and the fourth stages and less divergence in the second and then the first stages. For example, a tubular petal of *Helleborus thibetanus* undergoes the following developmental stages: a depression appear at the base of the blade, then two bulges appear at the base of the depression, and then the bulges fuse with one another to form the upper lip, the upper lip fuses with two margins of the blade that makes the petal oblique cup-shaped, the growth speed of the upper lip is faster than the two fused sides and that of the later is faster than the lower lip that makes the petal to be tubular; a spurred petal of *Aquilegia yabeana* undergoes the following developmental stages: a depression appears at the base of the blade, then two bulges appears at the base of the depression, the depression deepens to form the spur and the bulges stop further growth.

According to the molecular systematic results, the genera in two basal most clades, *Glaudidium* and *Hydrastis*, are apetalous. *Coptis* and *Xanthorhiza* are in the next basal most clade, the petal in this clade only has, or sometimes not clear, the depression at the base of the blade and the nectary tissue appears in the depression and the petals in these genera are not bilabial. The rest of the genera form the core Ranunculaceae in which two bulges appear at the base of the depression. The appearance of the bulges can be considered as a key innovation and let the petals get the diverged potential in morphology and finally resulted in the divergence of the genera.

The development processes of the petals in different petalous clades, or even in different petalous genera in the same clade, are different. The bulges might be lost in *Consolida* clade, in this case, the spur is well developed, or only one bulge appears in *Ranunculus* and *Nigella* clades, or both the bulges and the depression might be lost in *Adonis* which has the flat petals without nectary tissue.

The growth of the bulges which becomes the upper lip of the petal or the depression which becomes the succate or the spur can result in the hidden of the honey from the nectary tissue and thus can increase the difficulty for the nectar foraging pollinators and avoiding the non nectar foraging insects and then increase the pollination efficiency and increase the adaptability to different nectar foraging insects.

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POLLINATOR-MEDIATED SELECTION ON NECTARY DEPTH IN *UROPHYSA* (RANUNCULACEAE)

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Key words: *Urophysa, Apis cerana*, pollinator-mediated selection, nectary depth, petal evolution

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Pollinator-mediated selection has been considered to be one of major factors that shapes the evolution of flowers by matching flowers to their pollinators on traits associated with attraction of pollinators or mechanical fit. The match between nectary depth, which means the length of the tubular structure formed in many plant species to hide the nectary and store nectar, and the mouthparts length of its major nectar-foraging pollinators has been repeatedly demonstrated as an example, because this trait have shown a positive relationship with pollen removal and deposition in experimental manipulations in many synpetalous plants and orchid family. However, it remains unclear how pollinator-mediated selection affects the evolution of nectary depth in choripetalous and actinomorphic flowers, such as most flowers in Ranunculaceae. Here we investigated floral characteristics and pollinators in *Urophysa rockii* Ulbr. and *U. henryi* (Oliv.) Ulbr., as they are quite the same in habitat, anthesis and morphological characteristics except for nectary depth. Both of these species have flat white sepals and yellow petals each has a spatial structure at the base that contains nectar, but the nectary depth of *U. rockii* is deeper than that of *U. henryi*, for the former petals are shortly spurred about 3-4mm in length while the latter are saccate. Meanwhile, the flowers of both species are most frequently visited by *Apis cerana*, the Chinese honey bee, and one or two species of hover fly, Syrphidae, but only *A. cerana* was able to forage nectar in *U. rockii* while all visitors can forage nectar in *U. henryi*. *A. cerana* always lands on the center of a flower and projects its proboscis into each petal when its thorax touches anthers and stigmas. The difference between two species is that *U. rockii* was visited by *A. cerana* with a higher frequency, longer visiting time per flower and more activities on flowers than *U. henryi*. Besides, the petal width and its nectary depth of *U. rockii* closely match the width of the labrum and the effective mouthparts length of *A. cerana*, respectively. Therefore, we concluded that pollinator-mediated selection played a vital role in the evolution of nectary depth in *Urophysa*, with deeper nectaries favoured through reproductive fitness, because this trait affects flower-pollinator interaction and therefore pollen deposition. We also detected deeper nectaries favoured because this trait also affects nectar accumulation as well as deeper nectaries can prevent inefficiency visitors from foraging nectar effectively.

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CHOSEN ASPECTS OF FLOWERING OF RANUNCULACEAE REPRESENTATIVES IN POLAND

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Key words: Ranunculaceae, flowering phenology, floral sexual phases, flower abundance

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The family Ranunculaceae consists of numerous widespread species occuring from lowlands to subalpine or alpine zones. In Poland, the species grow in different types of habitats, including xerothermic swards (*Adonido-Brachypodietum, Brachypodio-Teucrietum, Thalictro-Salvietum, Seslerio-Scorzoneretum*) and decidous forests (*Tilio-Carpinetum*). Many species are popular ornamentals cultivated fro their esthetic value. Ranunculaceans vary remarkably in the phenology of blooming. Among them, there are early spring blooming species like *Eranthis hyemalis, Ficaria verna, Isopyrum thalictroides, Anemone nemorosa, A. ranunculoides*, and those that start to bloom in autumn, e.g. *Aconitum carmichaelli*. The overall flowering duration may differ significantly between years – for example, in *Anemone sylvestris* the disparities reached more than three weeks. The occurrence and the length of each blooming phase may vary considerably between sites, e.g. in *Adonis vernalis* 10-15-day dissimilarities in the occurrence of blooming stages were recorded. Additionally, the duration of the full blooming stage varied from 10 to 30 days.

The diurnal pattern of blooming among Ranunculaceae members was proved to be highly species-specific. Flowers of *Aquilegia vulgaris* started opening at approx. 5.00 (GMT+2), which was 2-3 hours earlier than those of *Adonis vernalis*. Significant differences in the diurnal flowering dynamics can be found even in the same genus: flowers of *Aconitum lycoctonum* began opening at 5.00 (with the peak between 6.00-9.00), while flowers of *Aconitum carmichaelii* started opening at 8.00 and peaked between 11.00-13.00.

The flowering abundance may differ among populations of the same species. The management type was found to have an impact on the individuals' density of *Adonis vernalis* occurring in xerothermic grasslands. The control of shrub encashment has already been designated as the factor determining the flowering abundance of *Adonis vernalis* in Lublin Upland.

Some Ranunculaceae representatives are dichogamous. This feature is commonly thought as the factor preventing self-pollination and inbreeding depression. For example, *Helleborus foetidus* and *Anemone sylvestris* are known to be protogynous, while many of the *Aconitum* representatives are protandrous. There may be evident difference in duration of each floral sexual phases, like in protandrous *Aconitum carmichaelii* (the length of male phase vs. female phase = 7.6 vs. 1.9 days, on average) or the time spent in stigma and pollen presentation can be similar, like in protogynous *Adonis vernalis* (7.5 and 8.4 days on average, respectively).

Disparities in flowering period, diurnal dynamics of blooming and sexual phases were found to be the adaptations to different insect foraging patterns.

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FLORAL REWARD IN RANUNCULACEAE SPECIES

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Key words: Ranunculaceae, nectar production, pollen production, floral phases, insect visitors

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Floral reward is important in ecological and evolutionary perspectives and essential in pollination biology. For example, floral traits, nectar and pollen features are essential for understanding the functional ecology, the dynamics of pollen transport, competition for pollinator services, and patterns of specialization and generalization in plant–pollinator interactions. We believe to present a synthetic description in the field of floral reward in Ranunculaceae family important in pollination biology and indicating connections between ecological and evolutionary approaches. The links between insect visitors' behaviour and floral reward type and characteristics exist.

Ranunculaceae is a family of aboot 1700 species (aboot 60 genera), distributed worldwide, however the most abundant representatives are in temperate and cool regions of the northern and southern hemispheres. The flowers are usually radially symmetric (zygomorphic) and bisexual, but in *Aconitum, Aquilegia* are bilaterally symmetric (zygomorphic). Most Ranunculaceae flowers offer no nectar, only pollen (e.g., *Ranunculus, Adonis vernalis, Thalictrum*), but numerous species create trophic niches for different wild pollinators (e.g. *Osmia, Megachile, Bombus, Andrena*) (Denisow *et al.* 2008).

Pollen is a source of protein, vitamins, mineral salts, organic acids and hormones, but the nutritional value varies greatly between different plant species. The pollen production can differ significantly between Ranunculacea species. The mass of pollen produced in anthers differ due to variations in the number of developed anthers. For example, inter-species differences are considerable, 49 anthers are noted in *Aquilegia vulgaris*, 70 anthers in *Ranunculus lanuginosus*, 120 in *Adonis vernalis*. A significant intra-species differences' in the number of anthers are also noted (e.g. 41 to 61 in *Aquilegia vulgaris*, 23-45 in *Ranunculus cassubicus*. Pollen production can be up to 62 kg per ha for *Ranunculus acer* on meadows.

Nectaries are secretory structures that synthesize and release nectar, a multi-component carbohydrate-rich aqueous solution. The relative location of nectaries within a flower is under pressure to maximize relations with pollinators, and hence to ensure the deposition of pollen on the stigma by pollinators. Nectaries are common in Ranunculaceae. Location, morphology and structure of the floral nectaries differ among Ranunculaceae representatives. Nectaries are tubular in *Helleborus* spp. or situated in nectary spurs (*Aconitum, Aquilegia*). Nectaries consist of an external epidermis, a photosynthesizing parenchyma, large branches of vascular tissue, a nectar-producing parenchyma, and an internal epidermis (Vesprini *et al.* 2008).

Nectar production is generally associated with mutualistic relations with animals that rely on sugar secretions in their nutrition. Inter-species differences in the amount of nectar produced and nectar chemistry are noted among Ranunculaceae species. Significant variations in nectar carbohydrate composition between male and female sexual phases occur both in the protandrous and protogynous flowers. In *Aconitum carmichaelii*, male-phase flowers produced 2.4-fold more nectar than female-phase flowers. Nectar sugar composition can differ between species within genera. The nectar can be sucrose-dominant, e.g. in *Aconitum carmichaelii* or sucrose-rich and lacking glucose in *A. lycoctonum* (Antoń & Denisow 2014). Variability in nectar production and/or carbohydrate composition in an individual plant may be considered to be evolutionarily significant. It can modify insect movements between flowers and plants, impact on visitation rates, reduce geitonogamy and thus increase plant fitness by cross-pollination. The floral morphology and the type of the floral attractant in *Anemone sylvestris* is an example of the in-between form from entomophily to anemophily (lack of nectar, papillous stigma, dense hairs situated between single carpels, small pollen grains – 10-25 μm, lack of balsam on the exine surface, starch accumulation in pollen).

In conclusion, the flower morphology and type of floral reward in Ranunculaceae species indicate the patterns for generalized insect visitors/pollinators (Apoidea bees, Coleoptera, Diptera) in actinomorphic species, for specialization towards bumblebees or show in-between form from entomophily to anemophily.

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NEW LOCALITY AND CONFIRMATION OF SOME HISTORICAL DATA FOR CRITICALLY ENDANGERED SOZOPHYTE *NIGELLA ARVENSIS* L. IN SOUTHERN POLAND

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Key words: Nigella arvensis, Poland, new locality, phytosociology

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Nigella arvensis L. is a rare archaeophyte which was previously recorded in 244 localities in Poland. It occurred in segetal associations and in vicinity of xerothermophilous thickets and grasslands. However in 21st century it was confirmed in only few localities (Piwowarczyk 2010; Ciosek & Cibor-Stefańska 2010; Zając & Zając 2014). The aim of our work was the description of three current localities and phytosociological identification of plots with *N. arvensis*. The sites were assigned to a square (10×10 km) on the ATPOL girds (Zając 1978). The new stand was found in Osiny (EE95). Two other localities were confirmed for Lisi Kamień hill near Szydłów (EF07) in Małopolska Upland, and for Salomin in Lubelska Upland (FE74). The plots were included in community of alliance *Caucalidion lappulae* R. Tx. 1950 and association *Vicietum tetraspermae* Kruseman et Vlieger 1939 em. Kornaś 1950.

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MORPHOLOGICAL FEATURES OF *DELPHINIUM SERGII* WISSJUL. *EX SITU* IN M.M. GRYSHKO NATIONAL BOTANICAL GARDEN

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Key words: Ranunculaceae, *Delphinium sergii*, morphological variability, polymorphism, heterophylly, ontogenesis

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Delphinium sergii Wissjul. is an endemic of eastern coast of Black Sea. It is listed in Red book of Ukraine with conservation status "vulnerable" (Didukh 2009). It grows mainly in eastern part of Ukraine in nature and is not typical for the Kyiv region. It is a perennial plant with bright blue flowers. The individuals of this specie are cultivated in the M.M. Gryshko National Botanical Garden during last 15 years. The results of the study of ontogenetic development and morphological diversity show that *D. sergii* is characterized by heterophylly and common morphological variability of leaf blade. The correlation of degree between leaf blade dissection and their formation and age was established. Dissected leaves are found to be "older" while with entire laminas – "younger". Formation of different leaves in individuals of the same age states their dependence from lighting, soil moisture, crop density, genetic heterogeneity and plasticity of individuals in different conditions of growth.

We observed a difference in terms of passing through ontogenetic stages among the individuals too. Our investigation established that the individuals of *D. sergii ex situ* can accelerate the ontogenetic development and reach the generative stage for just 2 years. The juvenile period in some individuals may last for just one growing season. It is noted that under the unfavorable factors (thickened crops, drought, and shading) development of *D. sergii* individuals became slower.

This species can be reproduced both by seed and vegetative. Propagation by seeds is the main way for distribution of these plants. Vegetative reproduction could be realized by particulation of individuals at *g* and *ss* stages. In Kyiv region *D. sergii* is blooming in June-July.

Delphinium is well known as such representing the "bee-flowers syndrome". According to our observations the main pollinators of *D. sergii* in conditions of our botanical garden were *Bombus pascuorum* (Scopoli, 1763), *B. hortorum* (Linnaeus, 1761), *B. lucorum* (Linnaeus, 1761), and *B. lapidarius* (Linnaeus, 1758). The flowers of *D. sergii* were attractive also for bees (*Lasioglossum* sp., *Apis mellifera* (Linnaeus, 1758)) and butterflies of *Ochlodes sylvanus* (Esper, 1778).

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AUTHOR INDEX

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The Ranunculaceae are often regarded as the most primitive of the herbaceous angiosperms. Some of the primitive characters found in the family are: numerous and spiral arrangement of floral parts, apocarpy, imperfect carpel closure, and follicles. However, many traits characterized as advanced are also common: finely dissected leaves, vessels with simple perforations, racemose inflorescences, unisexual flowers, zygomorphic flowers, specialized spurred petals, syncarpy (with each carpel still distinct), and achenes. So while some members of the family may be regarded as representative of the primitive condition, many others, in adapting to diverse environments, have developed «advanced» characters.

Sara B. Hoot, 1991

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