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The journal *Acta Botanica Universitatis Comenianae* publishes papers dealing with phytocoenology, plant biology and morphology, phytogeography, environmental botany, ecology and taxonomy of non-vascular and vascular plants. It is published twice per year. All published papers are reviewed.

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LET'S GO TO THE FIELD. BOTANICAL EXCURSION 7

POĎME SPOLU DO TERÉNU. BOTANICKÁ EXKURZIA 7

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Abstract

The seventh botanical excursion in the series “*Let's Go to the Field*” takes place in Bratislava, in the borough of Karlova Ves. The route leads from suburban areas into the mixed deciduous forests of the Devínska Kobyla Mts. The excursion focuses on hemerophilous taxa of cyanobacteria, algae, bryophytes, and fungi occurring in human-made and human-influenced habitats, as well as on hemerophobic species growing in forest biotopes. Among the species that are relatively rare in the Bratislava area, the bryophyte *Hylocomium splendens* was recorded.

Key words: Slovakia, Devínska Kobyla Mts., Bratislava, field practices in botany, non-vascular plants

Introduction

The present contribution builds upon a series of studies focused on botanical excursions conducted within the bachelor's and master's degree programs at the Faculty of Natural Sciences, Comenius University in Bratislava (Jančovičová et al. 2016, 2019, 2022; Mišíková et al. 2021, 2023; Pelechová-Drongová 2017). The excursion route is situated in the Karlova Ves borough of Bratislava, extending into the northeastern part of the phytogeographical unit Devínska Kobyla Mts. The primary objective is to document and demonstrate the diversity of non-vascular plants and fungi across environments with different degrees of anthropogenic influence, specifically urban zones, forest habitats, and transitional areas between urban and natural sites. The didactic framework of the excursion is based on the selection of taxa appropriate for teaching at both levels of university education.

During the excursion, students are introduced to selected representatives of bryophytes, lichens, and fungi that can be identified relative easily on the basis of macroscopic characteristics. In addition to forest species, urbanophilous taxa are also highlighted, distinguished by their frequent occurrence in anthropogenically modified environments. Special attention is devoted to species of ecological significance, whether due to their functional roles, indicator value, or distributional patterns. Most of the study area is

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covered by mesic deciduous forests dominated by hornbeam and oak (Šuvada 2023).

At the beginning of the excursion route, two notable landmarks can be seen: the Slovak Institute of Metrology (SMU, from the Slovak name *Slovenský metrologický ústav*) and the unfinished Cyclotron Center of the Slovak Republic (CCSR). The SMU, located near the “Karlova Ves” tram stop, occupies an area of 42,800 m² and is bordered by forests on the north, south, and west. It is the only institution in Slovakia that ensures the uniformity and accuracy of measurements of physical and technical quantities, using verified and calibrated measuring instruments as well as certified reference materials (Anonymous 1). The CCSR represented a large-scale scientific and medical project, initiated in 1997 in Bratislava, with the aim of applying cyclotron technology. Although approved by the Government of the Slovak Republic in 1999, the project was never brought to completion (Podhorský et al. 2004).

Material and Methods

Study area. The botanical excursion takes place in Bratislava, in the borough of Karlova Ves. The study area is a part of the phytogeographical unit of Devínska Kobyla Mts. (Futák 1984). The route of excursion includes three stops/sites designated as follows: (1) Institute of Metrology, (2) Forest Valley, and (3) Deciduous Forest (Fig. 1). A brief description of each site is provided in Tab. 1.

Tab. 1. Sites of the botanical excursion in the Karlova Ves borough of Bratislava.

Tree species highlighted in bold are dominant. Superscript numbers refer to the following sources: 1 – ISLHP (2025); 2 – Anonymous 2; 3 – Granec, Šurina (1999); 4 – Polák et al. (2011, 2012).

Site number	1	2	3
Site name	Institute of Metrology	Forest Valley	Deciduous Forests
Woody plants ¹	<i>Carpinus betulus</i> , <i>Quercus petraea</i> agg., <i>Q. cerris</i> , <i>Tilia cordata</i>	<i>Carpinus betulus</i> , <i>Fagus sylvatica</i> , <i>Quercus petraea</i> agg., <i>Tilia cordata</i>	<i>Fagus sylvatica</i> , <i>Quercus petraea</i> agg., <i>Carpinus betulus</i> , <i>Tilia cordata</i>
Forest age (years) ¹	105	50–125	60–120
Forest function ¹	Suburban and other forests with a significant health, cultural or recreational function		
GPS coordinates ²	48°09'59"N, 17°02'41"E	48°10'11"N, 17°02'24"E	48°10'05"N, 17°02'15"E
Elevation (m.a.s.l.) ²	220	260	330
Soils ³	Eutric cambisols to dystric cambisols, haplic umbrisols and skeletal umbrisols		
Bedrock ⁴	Granites, granodiorites		

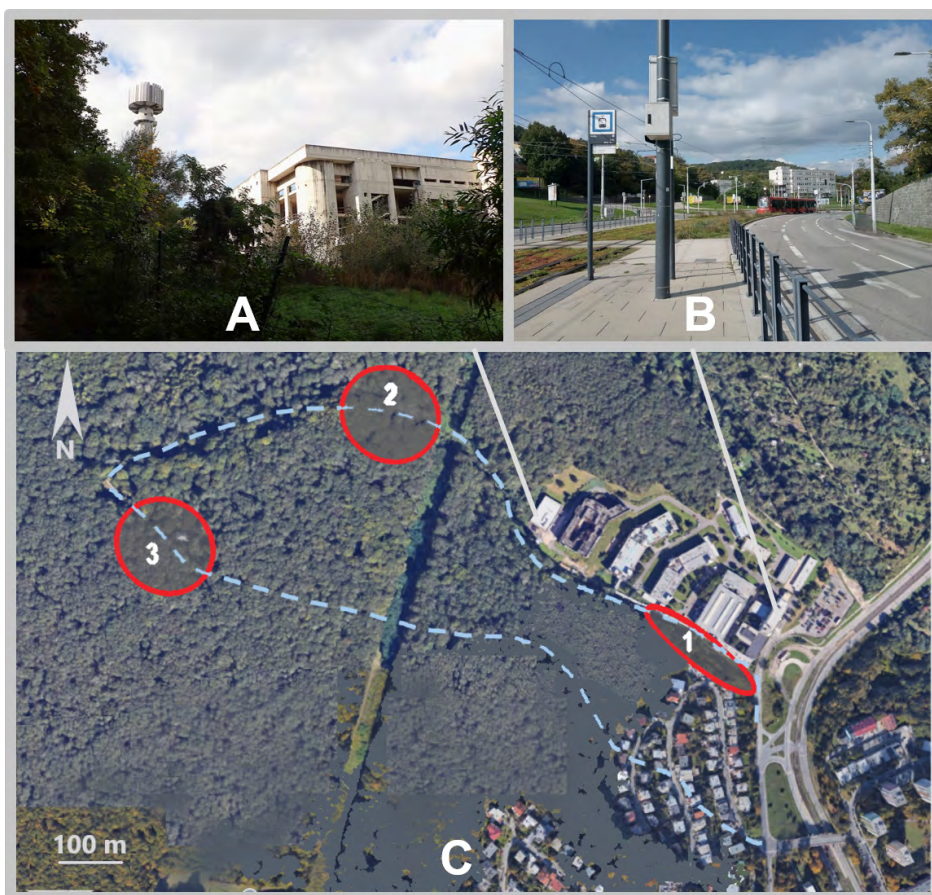


Fig. 1. Route of the botanical excursion in the Karlova Ves borough of Bratislava.

A – Abandoned buildings of the Cyclotron Center of the Slovak Republic (CCSR). **B** – Tram stop Kútiky and the Slovak Institute of Metrology (SMU). **C** – the route includes three stops/sites: **1** – Institute of Metrology, **2** – Forest Valley, and **3** – Deciduous Forest. Author: A and B – K. Mišíková. C – <https://www.freemap.sk>, modified by K. Mišíková.

Cyanobacteria, algae and lichenized fungi. Our field research focused exclusively on macroscopic, easily recognizable species. The nomenclature of cyanobacteria and algae follows Kaštovský et al. (2018a, b), the nomenclature of lichenized fungi is adopted from Anonymous 3 and Malíček et al. (2025).

Bryophytes. Bryophytes were collected from a variety of substrates. The majority of species were identified in the field based on their macromorphological characteristics. The nomenclature of bryophytes is derived from the study by Hodgetts et al. (2020).

Non-lichenized macroscopic fungi. Fruiting bodies were collected, identified and processed using standard mycological practices (e.g. Holec et al. 2012). The following works were mostly used for species identification: Knudsen, Vesterholt (2012), Læssøe, Petersen (2019), Ryvarden, Melo (2017), Jeppson (2018). Nomenclature follows the MycoBank database (<https://www.mycobank.org>). Microscopic mounts were

prepared in in Melzer's reagent or in Congo red after a short pre-treatment in a 5% KOH. The microscopic structures were observed, measured and photographed directly under an Olympus BX41 microscope. The size of microscopic structures was calculated based on 30 measurements per collection and presented as average $\pm$ standard deviation. After identification, some of the collections were preserved and deposited in the herbarium SLO (the herbarium of Comenius University in Bratislava, Faculty of Natural Sciences, Department of Botany).

Vascular plants. The nomenclature of vascular plants follows IPNI database (<http://www.ipni.org>).

Results and Discussion

i) Lists of recorded taxa

During excursions in the Karlova Ves borough of Bratislava, we identified one cyanobacterium, two algae, 29 bryophytes (two liverworts and 27 mosses), 11 lichenized fungi (Tab. 2), and 45 non-lichenized macroscopic fungi (Tab. 3).

Tab. 2. The list of cyanobacteria, algae, bryophytes and lichens recorded in the Karlova Ves borough of Bratislava.

Sites: 1 – Slovak Metrological Institute, 2 – Forest Valley, 3 – Deciduous Forest (for details on the sites, see Tab. 1).

Substrates: epg – epigeic species; epph – epiphytic species; epl – epilithic species; epx – epixylic species; ubi – ubiquitous species.

The nomenclature of bryophytes follows Hodgetts et al. (2020).

Species marked with an asterisk (*) are described in detail in the subsection "Annotated species".

Taxa/Sites	1	2	3
Cyanobacteria	Substrate		
<i>Nostoc commune</i> Vauch.	epg	–	–
Chlorophyta	Substrate		
<i>Trentepohlia umbrina</i> (Kützinger) Bornet	epph	epph	–
<i>Apatococcus-Desmococcus</i> complex	epph epl	epph	epph
Bryophytes	Substrate		
<i>Amblystegium serpens</i>	ubi	ubi	ubi
<i>Atrichum undulatum</i> *	epg	epg	epg
<i>Barbula unguiculata</i>	epg	–	–
<i>Brachytheciastrum velutinum</i>	epg	epg	epg
<i>Brachythecium rutabulum</i>	epg	epg epx	epg epx
<i>Ceratodon purpureus</i>	epg	–	–
<i>Dicranella heteromala</i>	–	epg	epg
<i>Funaria hygrometrica</i> *	epg	–	–
<i>Grimmia pulvinata</i>	epl	–	–
<i>Hedwigia ciliata</i>	–	epl	–
<i>Hylocomium splendens</i> *	epg	–	–

Taxa/Sites	1	2	3
<i>Hypnum cupressiforme</i>	ubi	ubi	ubi
<i>Lewinskya speciosa</i>	epph	epph	–
<i>Lophocolea coadunata*</i>	epg	–	–
<i>Lophocolea minor</i>	epg	–	–
<i>Orthotrichum anomalum</i>	epl	–	–
<i>Orthotrichum diaphanum</i>	epph epl	–	–
<i>Oxyrrhynchium hians</i>	epg	–	–
<i>Plagiomnium cuspidatum</i>	–	epg epX	–
<i>Plagiothecium nemorale</i>	–	epg	–
<i>Platygyrium repens</i>	–	epph	epg
<i>Pleurozium schreberi</i>	epg	–	–
<i>Polytrichum formosum*</i>	epg	epg	–
<i>Pterigynandrum filiforme</i>	–	epl	–
<i>Schistidium crassipilum</i>	epl	–	–
<i>Syntrichia ruralis</i>	epg epl	–	–
<i>Thuidium assimile</i>	epg	–	–
<i>Tortula muralis</i>	epl	–	–
<i>Tortula subulata</i>	epg	–	–
Lichenes	Substrate		
<i>Cladonia pyxidata</i> (L.) Hoffm.	epg	–	–
<i>Flavoplaca citrina</i> agg.	epl	–	–
<i>Kuettlingeria teicholyta</i> (Ach.) Trevis.	epl	–	–
<i>Myrsolecia dispersa</i> (Pers.) Šliwa, Zhao Xin et Lumbsch	epl	–	–
<i>Parmelia sulcata</i> Taylor	epph	epph	epph
<i>Physcia adscendens</i> (Fr.) H. Olivier	epph	–	–
<i>Physcia tenella</i> (Scop.) DC.	epph	epph	epph
<i>Protoparmeliopsis muralis</i> (Schreb.) M. Choisy	epl	–	–
<i>Rusavskia elegans</i> (Link) S.Y. Kondr. et Kärnefelt	epl	–	–
<i>Verrucaria nigrescens</i> Pers.	epl	–	–
<i>Xanthoria parietina</i> (L.) Th. Fr.	epph epl	epph	epph

Tab. 3. The list of macroscopic fungi recorded in the Karlova Ves borough of Bratislava.

Columns:

A – Taxa. Nomenclature follows the MycoBank database (<https://www.mycobank.org>).

B – Site. For more information on the sites, see Table 1.

C – Data on taxa published in Ripková, Kučera (2002). In that paper, the collecting site corresponded to our site no. 2.

D – Data on taxa collected during our study excursions, with herbarium numbers indicated for specimens deposited in the SLO herbarium.

Abbreviations: fb = fallen branch, ft = fallen trunk, sb = standing branch (attached to the trunk, i.e. not fallen on the ground), st = standing trunk, sp. = species (species not determined), *Car bet* = *Carpinus betulus*, *decid.* = *deciduous*, *Fag syl* = *Fagus sylvatica*, *Fra exc* = *Fraxinus excelsior*, *Prunus avium* = *Pru avi*, *Que pet* = *Quercus petraea*, *Sam nig* = *Sambucus nigra*

A Taxa	B Site	C Ripková, Kučera (2002)	D This study
<i>Agaricus bitorquis</i>	2	13.X.2002, soil detritus	
<i>Agaricus essettei</i>	2	13.X.2002, soil detritus	
<i>Auricularia auricula-judae</i> syn. <i>Hirneola auricula-judae</i>	2	13.X.2002, fb <i>Sam nig</i>	5.VI.2025, sb <i>Sam nig</i>
<i>Auricularia mesenterica</i>	3		5.VI.2025, ft decid. tree (SLO 2888)
<i>Bjerkandera adusta</i>	2	13.X.2002, ft <i>Car bet</i>	
<i>Boletellus pruinatus</i> f. <i>luteo-carnosus</i>	2	13.X.2002, soil detritus	
<i>Byssomerulius corium</i>	2	13.X.2002, fb <i>Que</i> sp.	
<i>Calocera cornea</i>	2	13.X.2002, fb decid. tree	
<i>Calycina citrina</i> syn. <i>Bisporella citrina</i>	3		27.V.2022, ft decid. tree (SLO 2883)
<i>Cerioporus squamosus</i> syn. <i>Polyporus squamosus</i>	3		24.IV.2025, ft <i>Fag syl</i>
<i>Cerioporus varius</i> syn. <i>Polyporus varius</i>	3		10.V.2004, fb <i>Fag syl</i> (SLO 2892); 27.V.2022, fb <i>Fag syl</i> ; 5.VI.2025, fb <i>Fag syl</i> (SLO 2881)
<i>Chlorociboria aeruginascens</i>	2		24.IV.2025, ft <i>Que</i> sp. (SLO 2886)
<i>Chorophyllum rhacodes</i> syn. <i>Macrolepiota rhacodes</i>	2	13.X.2002, soil detritus	
<i>Clitocybe nebularis</i>	2	13.X.2002, soil detritus	
<i>Clitopilus hobsonii</i>	2		27.V.2022, ft decid. tree (SLO 2891)
<i>Collybia odora</i> syn. <i>Clitocybe odora</i>	2	13.X.2002, soil detritus	
<i>Collybiopsis ramealis</i> syn. <i>Marasmiellus ramealis</i>	2	13.X.2002, ft <i>Que</i> sp.	
<i>Coprinopsis picacea</i> syn. <i>Coprinus picaceus</i>	2	13.X.2002, soil detritus	24.IV.2025, soil detritus

A Taxa	B Site	C Ripková, Kučera (2002)	D This study
<i>Crepidotus cesatii</i>	2	7.X.2002, 13.X.2002, ft <i>Que</i> sp.; 7.X.2002, fb <i>Fra exc</i>	
<i>Crepidotus caspari</i> syn. <i>Crepidotus lundellii</i>	2	13.X.2002, fb decid. tree	27.V.2022, ft decid. tree (SLO 2895)
<i>Crepidotus variabilis</i>	2	13.X.2002, fb <i>Que</i> sp.	5.VI.2025, fb decid tree (SLO 2902)
<i>Cyanosporus alni</i> agg. syn. <i>Oligoporus alni</i>	2	13.X.2002, ft decid. tree	
<i>Cyathus olla</i>	1		5.VI.2025, soil detritus (SLO 2893)
<i>Daldinia petriniae</i>	2		24.IV.2025, ft decid. tree (SLO 2882)
<i>Exidia nigricans</i>	2, 3	13.X.2002, fb <i>Fag syl</i>	24.IV.2025, fb <i>Fag syl</i>
<i>Fomes inzegae</i>	2, 3	13.X.2002, ft decid. tree	5.VI.2025, stump <i>Fag syl</i>
<i>Fomitopsis quercina</i> syn. <i>Daedalea quercina</i>	2	13.X.2002, stump <i>Que</i> sp.	
<i>Fomitoporia robusta</i> syn. <i>Phellinus robustus</i>	2		5.VI.2025, st <i>Que pet</i>
<i>Ganoderma lucidum</i>	2	13.X.2002, stump <i>Que</i> sp.	
<i>Geastrum triplex</i>	2	7.X.2002, 13.X.2002, soil detritus	
<i>Gymnopus dryophilus</i>	2	13.X.2002, soil detritus	5.VI.2025, soil detritus
<i>Gymnopus fusipes</i>	3		27.V.2022, near stump base <i>Que</i> sp.
<i>Hapalopilus rutilans</i> syn. <i>Hapalopilus nidulans</i>	2		27.V.2022, ft <i>Que</i> sp. (SLO 2899)
<i>Hymenochaete rubiginosa</i>	2		24.IV.2025, stump <i>Que</i> sp. (SLO 2894)
<i>Hymenopellis radicata</i> syn. <i>Xerula radicata</i>	2, 3	13.X.2002, decid. wood in soil	27.V.2022, decid. wood in soil (SLO 2890)
<i>Hypholoma fasciculare</i>	2		24.IV.2025, near stump base <i>Que</i> sp.
<i>Hypoxylon fragiforme</i>	3		24.IV.2025, fb <i>Fag syl</i>
<i>Hypsizygus tessulatus</i>	2	7.X.2002, near stump base <i>Que</i> sp.	
<i>Inocybe asterospora</i>	2	13.X.2002, soil detritus	
<i>Inocybe geophylla</i>	2	7.X.2002, soil detritus	
<i>Junghuhnia nitida</i>	2	7.X.2002, ft <i>Que</i> sp.	
<i>Laccaria amethystina</i>	2	13.X.2002, soil detritus	
<i>Lacrymaria lacrymabunda</i>	2	13.X.2002, soil detritus	
<i>Laetiporus sulphureus</i>	2		27.V.2022, st <i>Pru avi</i> ; 24.IV.2025, st <i>Pru avi</i>
<i>Lepiota clypeolaria</i>	2	13.X.2002, soil detritus	

A Taxa	B Site	C Ripková, Kučera (2002)	D This study
<i>Lepiota cristata</i>	2	7.X.2002, soil detritus	
<i>Lepista flaccida</i>	2	13.X.2002, soil detritus	
<i>Leucocortinarius bulbiger</i>	2	13.X.2002, soil detritus	
<i>Lycoperdon perlatum</i>	2	13.X.2002, soil detritus	
<i>Lycoperdon pyriforme</i>	2	13.X.2002, stump <i>Que</i> sp.	
<i>Macrolepiota procera</i>	2	13.X.2002, soil detritus	
<i>Marasmius rotula</i>	2	13.X.2002, fb decid. tree	
<i>Megacollybia platyphylla</i>	3		5.VI.2025, soil detritus
<i>Morchella esculenta</i>	2		24.IV.2025, soil detritus (SLO 2896)
<i>Mycena acicula</i>	2	13.X.2002, ft decid. tree	27.V.2022, fb decid. tree; 24.IV.2025, fb decid. tree
<i>Mycena alcalina</i>	2	13.X.2002, stump decid. tree	
<i>Mycena crocata</i>	2	13.X.2002, stump <i>Que</i> sp.?	
<i>Mycena galericulata</i>	2	13.X.2002, ft <i>Que</i> sp.	
<i>Mycena pelianthina</i>	2	7.X.2002, soil detritus	
<i>Mycena polygramma</i>	2	13.X.2002, soil detritus	
<i>Mycena pura</i>	2	7.X.2002, 13.X.2002, soil detritus	
<i>Mycena renati</i>	3		27.V.2022, fb <i>Fag syl</i> ; 24.IV.2025, fb <i>Fag syl</i>
<i>Mycena rosea</i>	2	7.X.2002, 13.X.2002, soil detritus	
<i>Pallidohirschioporus biformis</i> syn. <i>Trichaptum biforme</i>	3		27.V.2022, ft <i>Fag syl</i> ; 24.IV.2025, ft <i>Fag syl</i> (SLO 2905); 5.VI.2025, ft <i>Pru avi</i>
<i>Panellus stipticus</i>	2	13.X.2002, stump <i>Que</i> sp.	24.IV.2025, fb <i>Que</i> sp.
<i>Panus lecomtei</i> syn. <i>Panus rudis</i>	3		5.VI.2025, stump <i>Fag syl</i> (SLO 2885)
<i>Parasola conopila</i> syn. <i>Psathyrella conopilus</i>	3		27.V.2022, soil detritus (SLO 2900)
<i>Paxillus involutus</i>	2	13.X.2002, soil detritus	
<i>Phlebia rufa</i>	2		5.VI.2025, fb <i>Car bet</i> (SLO 2903)
<i>Neofavolus alveolaris</i> syn. <i>Polyporus mori</i>	2		10.V.2004, fb decid. tree (SLO 2879); 24.IV.2025, fb <i>Fra exc</i> (SLO 2884)
<i>Pluteus cervinus</i>	2, 3	13.X.2002, ft <i>Que</i> sp.	27.V.2022, stump decid. tree; 24.IV.2025, ft decid. tree; 5.VI.2025, ft <i>Que</i> sp. (SLO 2904)
<i>Pluteus ephebeus</i>	2	7.X.2002, soil detritus	

A Taxa	B Site	C Ripková, Kučera (2002)	D This study
<i>Pluteus phlebophorus</i>	3		10.V.2002, fb decid. tree (SLO 2901)
<i>Pluteus salicinus</i>	2	7.X.2002, ft <i>Que</i> sp.	
<i>Podofomes mollis</i> syn. <i>Datronia mollis</i>	3		5.VI.2025, fb <i>Fag syl</i> (SLO 2898)
<i>Radulomyces molaris</i>	2	13.X.2002, fb <i>Que</i> sp.	
<i>Rhodocollybia butyracea</i>	2	13.X.2002, soil detritus	
<i>Russula cyanoxantha</i>	2		27.V.2022, under <i>Fag syl</i> ; 5.VI.2025, under <i>Fag syl</i>
<i>Schizophyllum commune</i>	2, 3	13.X.2002, fb decid. tree	27.V.2022, fb <i>Fag syl</i> ; 5.VI.2025, fb <i>Fag syl</i>
<i>Steccherinum bourdotii</i>	2	13.X.2002, fb decid. tree	
<i>Stereum hirsutum</i>	2	13.X.2002, ft <i>Car bet</i>	5.VI.2025, fb <i>Car bet</i>
<i>Stereum subtomentosum</i>	2	13.X.2002, stump decid. tree	
<i>Trametes gibbosa</i>	3		5.VI.2025, stump <i>Fag syl</i>
<i>Trametes hirsuta</i>	3		24.IV.2025, ft <i>Fag syl</i> (SLO 2897)
<i>Trametes versicolor</i>	3		5.VI.2025, stump <i>Fag syl</i>
<i>Tricholoma bresadolae</i> syn. <i>Tricholoma bresadolatum</i>	2	7.X.2002, soil detritus	
<i>Tulostoma brumale</i>	1		27.V.2022, soil among moss <i>Syntrichia ruralis</i> (SLO 2880)
<i>Xerula pudens</i>	2, 3	13.X.2002, soil detritus	
<i>Xylaria longipes</i>	2	13.X.2002, ft decid. tree	27.V.2022, fb <i>Que</i> sp.; 24.IV.2025, fb <i>Car bet</i>
<i>Xylobolus frustulatus</i>	2		27.V.2022, ft <i>Que</i> sp.; 24.IV.2025, ft <i>Que</i> sp. (SLO 2889); 5.VI.2025, ft <i>Que</i> sp. (SLO 2887)

ii) Botanical excursion

The area used for presented botanical excursions (Fig. 1) is located near the Faculty of Natural Sciences and is easily accessible both on foot and by tram. In 2002, an excursion was also conducted here as part of a mycofloristic course, and the list of recorded species was published by Ripková, Kučera (2002). We incorporated this list into Tab. 3, where it can serve as a basis for comparison between the autumn aspect of fungi (documented during the mycofloristic course) and the spring–summer aspect (covered by our excursions). Even on the basis of just a few collection days (insufficient for a comprehensive assessment of the site's mycobiota), it is evident that in autumn the number of mycorrhizal fungi increases, particularly from families such as Boletaceae, Inocybaceae, Tricholomataceae, and others.

Mycologically, the Devínska Kobyla Mts. represent an attractive area; with more than 400 published taxa of macromycetes, it has been ranked as the sixth phytogeographical

unit of Slovakia in terms of fungal diversity (Ripková, Ďuriška 2009; Ďuriška 2010; Ďuriška et al. 2012). However, only a few published records exist from this particular part of the Karlova Ves borough, near the Slovak Institute of Metrology, and they are mostly those reported in the above-mentioned paper by Ripková, Kučera (2002). In the monograph on the Devínska Kobyla hills, based primarily on fungal collections made between the 1980s and the mid-1990s, Záhorovská (1997) reported only a single species, *Omphalotus olearius*, citing the locality as “K. Ves, nad Metrologickým ústavom.” It is therefore in our interest to continue botanical research in this area and to expand our knowledge of its biodiversity.

Site 1. Slovak Institute of Metrology – City meets the forest

The excursion route begins at the final stop of tram No. 9 in the Karlova Ves borough, heading towards the premises of the SMU. Along the left side of the road, a massive concrete wall is built. In urban environments, concrete surfaces serve as a significant substrate for competitively weaker organisms such as algae, bryophytes, and lichens, which start colonisation within a timeframe of several weeks to months (Perini et al. 2020; Cutler et al. 2013). However, macroscopic thalli of lichens and mosses typically develop after 2–6 years, depending on substrate properties and environmental conditions (Doulos et al. 2004; Veeger et al. 2025). On the wall near the SMU, species-rich and quantitatively abundant communities of bryophytes and lichenized fungi are differentiated. Mosses here are adapted to life on stony substrates primarily through their compact cushion-shaped growth forms (*Grimmia pulvinata*, *Orthotrichum anomalum*, and *Tortula muralis*), the dark pigmentation of gametophytes (*Schistidium crassipilum*, *T. muralis*), leaves terminating in elongated hair points (*Syntrichia ruralis*, *G. pulvinata*), as well as sporophytes with short setae immersed among the leaves (*G. pulvinata*, *S. crassipilum*). These functional adaptations allow urbanophilous species to persist in dry and warm microhabitats within cities. Among the lichenized fungi, conspicuous crustose thalli of *Flavoplaca citrina*, *Kuettlingeria teicholyta*, *Protoparmeliopsis muralis*, and *Verrucaria nigrescens* occur on the concrete surfaces.

The ecological roles and impacts of bryophyte and lichen cover on anthropogenic stone substrates remain a matter of debate. To some extent, lichens may contribute to the biodegradation of stone surfaces (Cozzolino et al. 2022). However, numerous authors emphasise the prevailing positive effects of epilithic bryophytes in urban settings, such as protecting surfaces from erosion, enhancing urban humidity, and trapping dust and pollutants within the thalli (Doulos et al. 2004, Spangler 2021, Żołnierz et al. 2022, Veeger et al. 2025). Mosses also represent important microhabitats and construction material for other organisms, while from an aesthetic perspective, they enhance human well-being (Gabrys 2012, Gładalski et al. 2021).

Along the edges of the concrete-panel road running beside the wall, several pioneer species occur, colonizing exposed bare soil and thereby initiating succession in brownfields, construction sites, roadsides, and tram tracks. Among cyanobacteria, the macroscopic terrestrial *Nostoc commune* is present, while bryophyte colonizers include *Barbula unguiculata*, *Ceratodon purpureus*, *Funaria hygrometrica*, and *Syntrichia ruralis*. Only a few meters further, the wall ends, and an oak forest appears on the left side.

On top of the concrete wall, in a layer of soil among the mosses, the long-stemmed puffballs attract attention. Here one can find *Tulostoma brumale*, a fungus with rather

pale, slender fruiting bodies and a brown zone around the projecting opening. Continuing further along the path, on the soil at the edge of the trail, cup-shaped, greyish fruiting bodies of *Cyathus olla* may be encountered; their outer surface is felty to almost glabrous, while the inside is smooth and contains lens-shaped peridioles.

In close proximity to residential buildings within this oak stand, characteristic forest taxa including *Atrichum undulatum*, *Dicranella heteromala*, *Plagiothecium nemorale*, and *Polytrichum formosum* coexist with species typical of forest edges and less dense woodlands, e.g., *Hylocomium splendens*, *Lophocolea coadunata*, *Pleurozium schreberi*, and *Thuidium assimile*. On clayey slopes along the forest path, abundant populations of the lichen *Cladonia pyxidata* develop, with conspicuous cup-shaped podetia. The bark of oak trees frequently hosts aerophytic algae of the *Pleurococcus–Apatococcus* complex, resulting in a green coloration, as well as nitrophilous lichens, e.g., *Physcia adscendens*, *P. tenella*, and *Xanthoria parietina*.

Site 2. Forest Valley – Into the woods

At the CCSR, the former concrete road transforms into a forest path, which passes through overgrown clear-cut areas and leads to the entrance of a valley within deciduous forests. On the steep slopes, the vascular plant understory is only weakly developed; however, dense carpets of forest mosses such as *Atrichum undulatum*, *Brachythecium rutabulum*, *Hypnum cupressiforme*, *Plagiomnium cuspidatum*, and *Polytrichum formosum* are locally abundant. Scattered rocky boulders also occur in the area, providing suitable microhabitats for ubiquitous or epilithic bryophytes including *Amblystegium serpens*, *Brachytheciastrum velutinum*, *Hedwigia ciliata*, *H. cupressiforme*, and *Pterigynandrum filiforme*.

In the valley, with an abundance of fallen branches, lying trunks, and a thick layer of litter, several fungal species find suitable conditions. Excursions are particularly rewarding after rainfall, when the water-soaked substrates stimulate the formation of fruiting bodies. Among the recorded species, students were especially interested in, for example *Chlorociboria aeruginascens* that stains the substrate green and, under suitable conditions, forms small green apothecia with a somewhat felty outer surface. The asci are amyloid (staining blue in Melzer's reagent), 8-spored, and measure $56.5\text{--}67.5 \times 3.7\text{--}4.2\text{ }\mu\text{m}$. The one-celled, somewhat allantoid, hyaline spores measure $5.6\text{--}7.1 \times 1.3\text{--}1.8\text{ }\mu\text{m}$.

Coprinopsis picacea, in English Magpie Inkcup, in Slovak *hnojník strakatý*, is a large coprinoid species characterized by persistent, adpressed, pale brown to almost white veil scales on a grey-brown pileus surface. The epithet refers to its appearance and is derived from the Latin name of the bird *Pica pica* – in English *Eurasian magpie*, in Slovak *straka obyčajná*.

Among the several *Mycena* species recorded at this site, two are particularly striking in their coloration: a medium-sized *Mycena renati* with a pink pileus, yellow stipe and a nitrous odor, and a small, inodorous *M. acicula* with an orange pileus and yellow stipe.

Xylobolus frustulatus – a perennial, whitish to grey-brown corticioid up to 2 mm thick. It is commonly known as “the ceramic fungus” (en.wikipedia.org) because its fruitbodies form small, hard, flat, crust-like aggregations that resemble broken pieces of ceramic tile (Fig. 2). Microscopically, the context is monomitic, the hyphae are thick-walled and echinulate-verrucose cystidia (acanthohyphidia) are characteristic (Fig. 2).



Fig. 2. *Xylobolus frustulatus*: left – basidiomata, right – acanthohyphidia 5 μm wide (stained in Congo red). Bratislava, the borough of Karlova Ves, 2025. Author: S. Jančovičová.

Site 3. Deciduous Forests – Life after life

The final part of the excursion follows the red-marked tourist trail (Cesta hrdinov SNP), running approximately along the contour line through mixed deciduous forests. Due to the dense understory, bryophytes occur only sporadically, most frequently on decaying wood, where species such as *Amblystegium serpens*, *Brachythecium rutabulum*, and *Hypnum cupressiforme* are recorded.

At the final site, we can focus on the fungal spectrum occurring on large fallen trunks of beech (*Fagus sylvatica*). For example, the sessile pilei of *Pallidohirschioporus biformis* grow in large numbers, overlapping each other like a roof, and are difficult to overlook. This species, commonly known as “the violet-toothed polypore” (en.wikipedia.org), is an annual polypore with rather pale, concentrically zonate pilei, sometimes violet at the margin and greenish from algal growth near the point of attachment to the substrate. The violet hymenophore is initially poroid with 2–4 pores per mm, but with age the pores disintegrate to form “teeth” (Fig. 3).

Basidiomata of *Panus rudis* grew on the cut surface of a *Fagus sylvatica* stump with a diameter of approximately 120 cm. The basidiomata no longer exhibited the characteristic rosy tint, but the rigid hairs on the surface were still distinct (Fig. 4). The pleurocystidia are thick-walled and measure $42.7\text{--}57.1 \times 10.5\text{--}13.4 \mu\text{m}$ (Fig. 4).

Although both species belong to the same genus and share a dark brown to black stipe base by which they attach to the woody substrate, they differ clearly in other characters. *Ceriporiopsis squamosus* may develop a pileus up to 500 mm wide, with adpressed, coarse scales on the surface and angular pores 1–2 mm in diameter. in contrast, *C. varius* has smaller pilei, 20–120 mm wide, with a smooth or slightly streaked surface and small, rounded pores, 6–9 per mm.

When we encounter fruiting bodies of the genus *Fomes* at this site, we can pause to discuss the concept of cryptic species. According to Peintner et al. (2019), these are species that cannot be easily distinguished based on morphology, but form distinct phylogenetic lineages according to molecular markers. *Fomes fomentarius* and *F. inzengae* are examples of such species: they are morphologically indistinguishable



Fig. 3. *Pallidohirschioporus biformis*: left – upper surface of basidiomata, right – lower surface of basidiomata with violet hymenophore of tubes to teeth. Bratislava, the borough of Karlova Ves, 2025. Author: S. Jančovičová.



Fig. 4. *Panus rudis*: left – basidiomata, right – pleurocystidia 12 µm wide (stained in Congo red). Bratislava, the borough of Karlova Ves, 2025. Author: S. Jančovičová.

but are genetically clearly separated (Peintner et al. 2019). The results of a study by Tomšovský et al. (2023) conducted in the South Moravian region of Czechia (Central Europe) revealed the ecological preferences of *Fomes* species along an altitudinal gradient. *Fomes fomentarius* is predominantly distributed at higher altitudes (400–970 m a.s.l.), where beech (*Fagus sylvatica*) and birch (*Betula* spp.) are its main hosts. In contrast, *F. inzengae* occurs mainly in lowland areas (154–490 m a.s.l.) and exhibits a broad host range, including *Acer*, *Aesculus*, *Alnus*, *Betula*, *Fagus*, *Fraxinus*, *Quercus*,

Platanus, *Populus*, *Salix*, *Sorbus*, and *Tilia*. Gáperová et al. (2025) found that the two *Fomes* species occur across almost all of Europe and show no clear geographical segregation. However, they exhibit different host preferences. There are five host genera shared by both fungal species: *Acer*, *Alnus*, *Betula*, *Fagus*, and *Populus*. Our records of *Fomes* fruiting bodies from the studied area in the Karlova Ves borough of Bratislava (60–120 m a.s.l.) were identified as *F. cf. inzengae* in accordance with Tomšovský et al. (2023).

At both sites, 2 and 3, species can be found that demonstrate deeply rooting stipes: *Gymnopus fusipes* and *Hymenopellis radicata* (Fig. 5). On this occasion, it should be emphasized that all fungi must be carefully removed from the substrate to avoid losing important diagnostic characters.

iii) Annotated species

Atrichum undulatum (Fig. 6A) and *Polytrichum formosum* (Fig. 6B) of the class Polytrichopsida are among the most common acrocarpous, terrestrial bryophytes in Central European forests. Due to their unique characteristics, both are relatively easy for beginners to identify.

A. undulatum forms loose, green to brown-green tufts. Individual stems are erect, unbranched, to 5 cm high, with lanceolate, narrow leaves up to 1 cm long (Rumsey 2010a). A key identifying feature is the strong transverse undulation of the moist leaves, which become crisped when dry. The leaf margins are toothed, with the nerve



Fig. 5. *Hymenopellis radicata*: left – basidioma growing from soil detritus, right – basidioma with a deeply rooting stipe. Bratislava, the borough of Karlova Ves, 2025. Author: S. Jančovičová.

extending to the leaf tip. Capsules are frequent, inclined, narrowly cylindrical, 3–4 mm long, on 2–4 cm long reddish seta. The calyptra is smooth and translucent. *A. undulatum* is widespread in woodlands, favoring shaded, well-drained sites, but also thrives in unimproved grasslands, on banks, and on rocky ledges. *Atrichum* species are valued in practices like moss and bonsai gardening for their ability to prevent soil erosion and retain moisture (Glime 2007).

P. formosum is a medium-sized moss with erect, unbranched shoots that grow in loose tufts, typically 5–10 cm tall. Its dark green, straight leaves are approximately 1 cm long and feature narrow, colorless, and distinctly toothed margins. The nerve is very wide, with 70 longitudinal lamellae on the upper surface (Rumsey 2010b). Capsules are 4- to 6-angled, erect to inclined, on a long seta (4–10 cm). When young, the capsule is covered by a distinctive hairy calyptra. *P. formosum* is typical in deciduous lowland woodlands on acidic to nearly neutral soils. *Polytrichum* species are often used in moss gardens, and their firm and rigid shoots have been utilized to make brooms and mats. Historically, the hairy calyptra was used in traditional medicine under the Doctrine of Signatures to strengthen hair (Glime 2007). Furthermore, its sensitivity to pollutants renders it an important bioindicator for environmental assessment (Korzeniowska 2022).

Funaria hygrometrica (Fig. 6C) is a cosmopolitan ephemeral species highly adapted to colonize recently burned or disturbed ground, often completing its life cycle in a few months. Its appearance is highly variable but easily recognized when its sporophyte is present. The plants are autoicous and can also reproduce vegetatively (Hodgetts 2010). The leaves are ovate, translucent, and 2–4 mm long with large, loose cells. Asymmetrical, curved capsules are typically abundant, borne on a long (3–5 cm), peculiarly twisted seta and covered by a large, translucent calyptra. This nitrophilous species is common in ruderal habitats like gardens, waste places, roadsides, and old fireplaces.

Hylocomium splendens is an epigeic, large, conspicuous moss that forms extensive, glossy bright green to yellow-green carpets. Its shoots, 5–20 cm long, are characteristically branched and feature an „etage“ growth pattern, often producing one new layer per year. The stems are reddish, and the stem leaves are oval with a long tip (2.5–3 mm long). Capsules are rarely formed. It grows in forests, rock terraces, forest road banks, occasionally on rotting wood. *H. splendens* was historically used for livestock bedding and as insulation in traditional wooden houses. Currently, it is a key species in biomonitoring studies, it is also used as packaging material and for growing epiphytic plants (Glime 2007).

Lophocolea coadunata (Fig. 6D) is an easily recognizable foliose liverwort. Its stems are delicate, translucent, and strongly aromatic. The pale green shoots (2–5 cm long) have conspicuously bilobed leaves (approx. 2 mm long) and similarly bilobed underleaves, which are visible with a hand lens. *L. coadunata* grows primarily on soil in woodlands and grasslands. It should be noted that this taxon is not always distinguished from the broader species *L. bidentata* (Vána 2017).



Fig. 6A – *Atrichum undulatum*, 6B – *Polytrichum formosum*, 6C – *Funaria hygrometrica*, 6D – *Lophocolea coadunata*. Bratislava, the borough of Karlova Ves, 2025. Author: K. Mišíková.

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Abstrakt

Siedma botanick  exkurzia zo s rie „Pod me do ter nu“ sa kon  v Bratislave, v mestskej  asti Karlova Ves. Trasa vedie zo z stavbov ch oblast  do zmiezan ch listnat ch lesov Dev nskej Kobyly. Exkurzia je zameran  na hemerofiln  tax ny sin c, rias, machorastov a h b, ktor  sa vyskytujú v  lovekom vytvoren ch a  lovekom ovplyvnen ch biotopoch, ako aj na hemerof bne druhy rast ce v lesn ch biotopoch. Z druhov, ktor  s  v bratislavskej oblasti pomerne zriedkav , bol zaznamenan  machorast *Hylocomium splendens*.

K   ov  slov : Slovensko, Dev nska Kobyly, Bratislava, praktick  cv chenia z botaniky, n   ie rastliny

A SURVEY OF BRYOPHYTES ON CALVARY HILL IN BRATISLAVA (OLD TOWN BOROUGH)

PREHLAD MACHORASTOV KALVÁRSKEHO VRCHU V BRATISLAVE (MESTSKÁ ČASŤ STARÉ MESTO)

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Abstract

This study presents the first bryological survey of Calvary Hill, a forest fragment located in the urbanized Old Town borough of Bratislava (Slovakia). A total of 50 bryophyte species were recorded, including three liverworts and 47 mosses. One red-listed species, *Rhynchostegium rotundifolium* (EN), was observed. The bryophyte flora was dominated by apophytic and urban-tolerant species (42% to 47%), while forest specialists (8%) occurred only rarely. Three sampling sites (SS) were established at the locality. The highest species richness (45 species) was found in the largest sampling site (SS I), while ongoing restoration activities negatively affected diversity in SS III (33 species). Comparison with a nearby urban woodland (Horský park) revealed low floristic similarity, highlighting the unique character of Calvary Hill. In terms of substrate preference, epigeic (24) and epiphytic (21) species dominated. Within the life strategies, colonists (58%-67%) and perennials (26%-24%) were most frequently represented. The intensity of anthropogenic impact (HI) was relatively high in terms of species composition, as almost half of the species tolerated moderate to high HI. Despite urban pressures, the site serves as a biodiversity refuge and underscores the importance of conserving small forest remnants within city landscapes.

Key words: mosses, liverworts, urban ecology, forest fragments, biodiversity, Central Europe

Introduction

Woodland fragments within urban environments represent important biodiversity hotspots for various groups of organisms. These remnants provide long-term refugia for hemerophobic species under altered environmental conditions and simultaneously offer novel ecological niches for species that are less sensitive – or even insensitive – to urbanization pressures (Honnay et al. 1999, Reháčková et al. 2007). In human-modified landscapes, forest fragments fulfill important ecological functions and services. They serve as accessible recreational areas, contribute positively to microclimate, and act as sources of diaspores (Tyrväinen et al. 2004). However, woodland fragmentation often results in reduced species richness and population sizes, altered community structure

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and microclimatic conditions, and limitations in species dispersal (Pharo et al. 2004). Within the Old Town borough of Bratislava, despite its urban context, several forested areas were preserved. Among the largest are the protected areas Horský park and Bôrik, the steep slopes above Mlynská dolina, and Calvary Hill.

Historically, the locality Calvary Hill was not forested. It was composed of vineyards, meadows, pastures, and xerothermic habitats with scattered trees and shrubs (Horváth 1990, Letz 2000, Szilágyi 2000, Hrnčiarová 2016). In 1694, one of the first Stations of the Cross in the Kingdom of Hungary was constructed here to commemorate the 1683 victory over the Turks at the Battle of Vienna (Anonymus 1). The first significant structures built in the area were two chapels constructed in the early 18th century. The larger of these was later replaced by the Church of Our Lady of the Snows, built between 1943 and 1948 (Reháčková et al. 2007, Reháčková 2008).

Following World War II, the site was subject to neglect, leading to the expansion of invasive tree species, notably *Robinia pseudoacacia*. In recent years, reconstruction and restoration activities have resumed, particularly focusing on the Stations of the Cross and the top-hill area (Anonymus 1).

The present study provides the first comprehensive inventory of bryophyte species occurring on Calvary Hill, highlighting its role as a significant biodiversity refuge within the urban environment of Bratislava.

Methods

The forest stand on Calvary Hill covers an area of 4.78 ha, and is located on the northern boundary of the Old Town borough in Bratislava (Fig. 1). The locality is bordered by Pražská, Langsfeldova, and Ostravská streets, with coordinates 48°09'38.1"N, 17°05'59.6"E (measured cca. in the centre of the locality) and an elevation ranging from 200 to 260 m a.s.l. The geological bedrock consists of biotite and muscovite-biotite granodiorites (Polák et al. 2011, 2012).

According to Reháčková et al. (2007), plant communities of the *Carpinion betuli* Issler 1931 alliance are present in the area. The most frequent tree species include *Acer platanoides*, *A. campestre*, *Carpinus betulus*, *Fraxinus excelsior*, *Pinus sylvestris*, *Quercus petraea* agg., *Robinia pseudoacacia*, *Tilia cordata*, *T. platyphyllos*, among others. The herb and shrub layers are well developed; at sampling site (SS) I, *Hedera helix* forms a continuous cover in some places. A small remnant of oak forest is preserved in the western part of the locality. Currently, restoration activities are ongoing, particularly on the hill-top (SS III) and along the Stations of the Cross (Anonymus 1).

Field research was conducted from March to June 2025. The study area was divided into three sampling sites (SS), namely: SS I – slopes above Pražská street, with northern to northeastern orientation, covering 3.69 ha; SS II – remnant oak stand with western exposure, covering 0.57 ha; SS III – summit plateau and southern to southeastern slopes, covering 0.48 ha. At each site, bryophyte species were surveyed across all available substrates.

Bryophyte nomenclature follows Hodgetts et al. (2020), and vascular plant names are cited according to the International Plant Names Index (IPNI 2025). Conservation status of mosses is based on the Slovak Red List (Mišíková et al. 2020). Ellenberg indicator

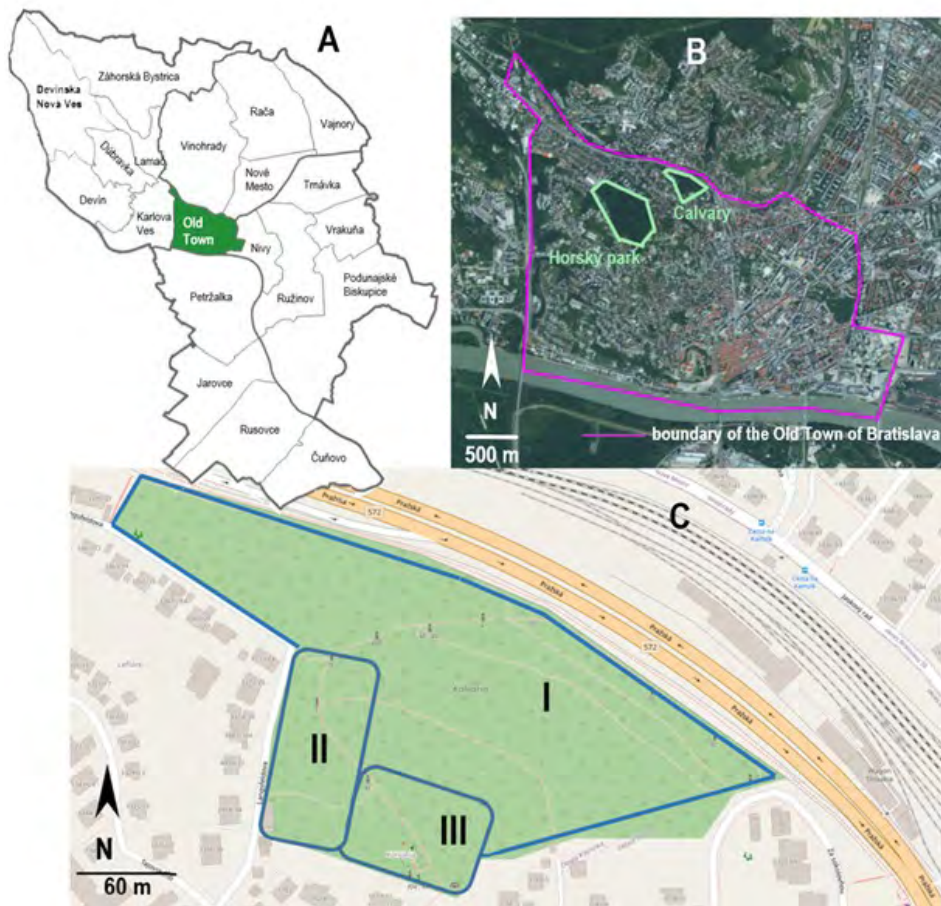


Fig. 1. Map of Calvary Hill in Bratislava. A. Boroughs of Bratislava. B. Forest fragments Calvary Hill and Horský park in Old Town borough. C. Sampling sites on Calvary Hill; I – slopes above the Pražská street, II – remains of oak stand, III – the top part of the Calvary Hill. (Source: A – orig. K. Mišíková; B, C –<https://www.freemap.sk>, modified by K. Mišíková).

values (EIV) are taken from Ellenberg et al. (1991), while nitrogen (N) values follow Simmel et al. (2021), who consider them indicators of overall habitat nutrient status. Life strategies (LS) follow Dierßen (2001). The degree of human impact (HI) (hemeroby) was assessed according to Dierßen (2001), Kürschner (2004), Kürschner et al. (2007), and Puglisi et al. (2012). The affinity of bryophytes to forest habitats was classified into the following categories (Bernhardt-Römermann et al. 2018): M1.1 – species largely restricted to closed forest, M1.2 – species preferring forest edges and clearings, M2.1 – species occurring both in forests and open habitats, M2.2 – species that may occur in forests but prefer open land.

For the statistical analyses and graph visualizations, the statistical software XLSTAT v. 2025 (Addinsoft, Paris, France) was used. Differences in species composition, substrate preference, and EIV among the three sampling sites were analyzed using non-parametric

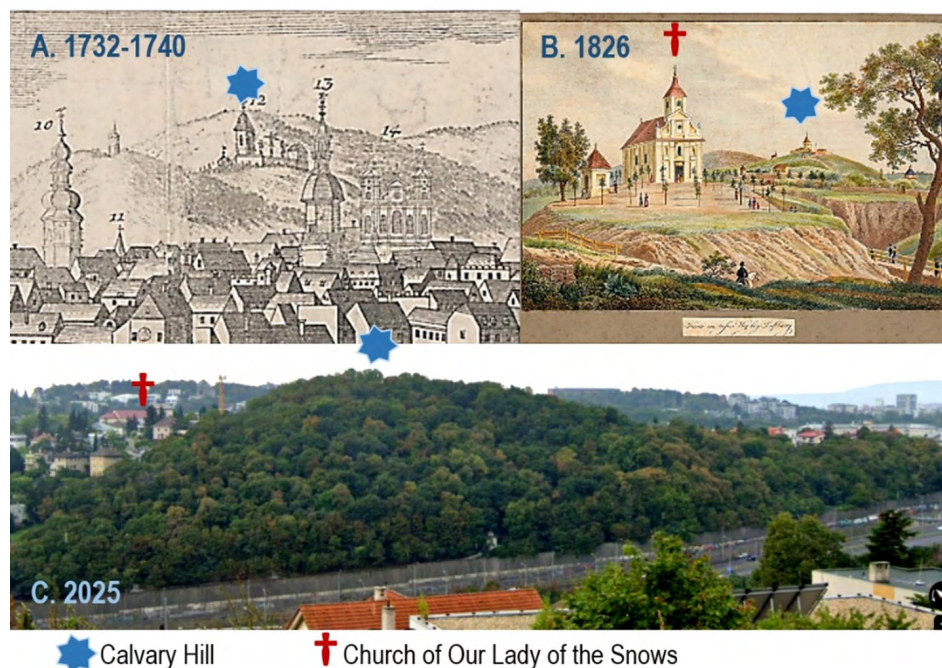


Fig. 2. Calvary Hill in Bratislava across historical periods. A. Depiction of Bratislava, created by Friedrich Bernhard Werner and Johann Friedrich Probst, dated between 1732 and 1740 (source: <https://slovakiana.sk/kulturne-objekty/cair-ko1lfj1>). B. The Church of Our Lady of the Snows, created by Jozef Anton Lántz and Matthias Trentsensky, dated 1826 (source: https://www.webumenia.sk/dielo/SVK:GMB.C_7701). C. Contemporary view (2025) of Calvary Hill, slopes above Pražská street, viewpoint from Chrástová street (source: <https://www.google.com/maps/>).

ANOVA (Kruskal-Wallis test), followed by Dunn's post hoc multiple comparisons ($\alpha \leq 0.05$). The Jaccard index (Jc) (Jaccard 1908) was used to assess species composition similarity between Calvary Hill and the nearby forested area Horský Park.

Results and Discussion

A total of 50 bryophyte taxa were recorded on Calvary Hill, comprising three liverworts and 47 moss species (Table 1, Fig. 4A). Among them, the red-listed species *Rhynchostegium rotundifolium* (EN) was found in SS I, growing on small stones (Fig. 3C, D). The bryophyte flora was dominated by apophytic and urbanophilous species such as *Amblystegium serpens*, *Brachythecium rutabulum*, *Ceratodon purpureus*, *Funaria hygrometrica*, *Grimmia pulvinata*, *Orthotrichum anomalum*, *Schistidium* spp., and *Tortula muralis*. Frequent epiphytes included *Lewinskya speciosa*, *Nyholmiella obtusifolia*, and *Orthotrichum diaphanum*. In contrast, typical forest specialists such as *Dicranella heteromalla*, *Polytrichum formosum*, and *Plagiothecium cavifolium* were rare.



Fig. 3. Calvary Hill in Bratislava. **A.** Anthropogenic stone substrates above Pražská street (SS I). **B.** Remains of oak stand (SS II). **C.** Habitat of *Rhynchostegium rotundifolium* (SS I). **D.** *R. rotundifolium*. **E.** Epiphytic bryophytes (primarily the genus *Lewinskya*), together with the predominantly epilithic moss *Grimmia pulvinata* (SS II). (Source: orig. K. Mišíková).

Species richness and composition in urban woodlands can be influenced by a variety of ecological and anthropogenic factors. Among the most significant are the patch size, stand age, structural heterogeneity, microclimatic conditions, air quality, and tree species composition (Gignac, Dale 2005; Mežaka et al. 2018; Fudali, Żołnierz 2019).

Of the three SSs, SS I harbored the highest number of bryophyte species ($n = 45$), likely due to its larger area and diverse microhabitats, while SS III exhibited the lowest diversity ($n = 33$), affected by ongoing reconstruction and canopy modifications. Significant differences in species composition were found between SS I and SS III (Kruskal-Wallis test, $p = 0.004$, $\alpha \leq 0.05$).

Tab. 1. List of recorded species on Calvary Hill in Bratislava. Species: (H) – liverwort. Sampling site: I - slopes above the Pražská street, II - remains of oak stand, III - the top part of the Calvary Hill. Substrate: epg – epigeic species, epl – epilithes, epvh – epiphytes, epv – epixylic species. Species abundance: 3 – frequent species (more than 7 records), 2 – sporadic species (2 – 6 records), 1 – rare species (1 – 2 records).

Species	Sampling site, substrate			Species abundance
	I	II	III	
<i>Amblystegium serpens</i>	epg epl epvh epv	epg epl	epg epl epvh	3
<i>Atrichum undulatum</i>	epg	epg	epg	2
<i>Barbula unguiculata</i>	epg	epg	epg	2
<i>Brachytheciastrum velutinum</i>	epg epl epvh epv	epg epl	epg epl	3
<i>Sciuro-hypnum populeum</i>	epl	-	epl	2
<i>Brachythecium rutabulum</i>	epg epl epvh epv	epvh epv	epg epvh	3
<i>Brachythecium salebrosum</i>	epl	-	-	1
<i>Bryum argenteum</i>	-	-	epg	1
<i>Bryum dichotomum</i>	epg	epg	-	1
<i>Ceratodon purpureus</i>	epg epl	epg epl	epg	3
<i>Dicranella heteromalla</i>	epg	epg	epg	1
<i>Dicranoweisia cirrata</i>	epvh	-	-	1
<i>Didymodon fallax</i>	epg	-	epg	1
<i>Frullania dilatata</i> (H)	-	epvh	epvh	1
<i>Funaria hygrometrica</i>	epg	epg	epg	3
<i>Grimmia pulvinata</i>	epl	epl epvh	epl	3
<i>Hypnum cupressiforme</i>	epg epl epvh epv	epg epl epvh epv	epg epl epvh epv	3
<i>Kindbergia praelonga</i>	epg	-	-	1
<i>Leskea polycarpa</i>	epvh	epvh	epvh	2
<i>Lewinskya affinis</i>	epvh	epvh	epvh	2
<i>Lewinskya speciosa</i>	epvh	epvh	epvh	3
<i>Marchantia polymorpha</i> (H)	epg	-	-	1
<i>Nyholmiella obtusifolia</i>	epvh	epvh	epvh	3
<i>Orthotrichum anomalum</i>	epl	epl	epl	3
<i>Orthotrichum diaphanum</i>	epl epvh	epvh	epl epvh	3
<i>Orthotrichum pumilum</i>	epvh	epvh	epvh	1
<i>Orthotrichum stramineum</i>	epvh	epvh	epvh	1
<i>Ptychostomum capillare</i>	epg epl	epg	-	3
<i>Ptychostomum imbricatum</i>	epl	epg epl	epg	2
<i>Ptychostomum moravicum</i>	epvh	epvh	epvh	2
<i>Ptychostomum rubens</i>	epg	-	-	1
<i>Oxyrrhynchium hians</i>	epg	epg	epg	2
<i>Plagiomnium cuspidatum</i>	epg	epg	-	2
<i>Plagiothecium cavifolium</i>	epg	epg	-	1

Species	Sampling site, substrate			Species abundance
	I	II	III	
<i>Platygyrium repens</i>	epph	epph	-	2
<i>Pleuridium subulatum</i>	epg	-	-	1
<i>Polytrichum formosum</i>	epg	epg	-	1
<i>Pulviger a lyellii</i>	-	epph	epph	2
<i>Pylaisia polyantha</i>	epph	epph	-	1
<i>Radula complanata</i> (H)	epph	epph	-	1
<i>Rhynchostegium murale</i>	epl	epl	epl	2
<i>Rhynchostegium rotundifolium</i>	epl	-	-	1
<i>Schistidium apocarpum</i>	epl	-	-	2
<i>Schistidium crassipilum</i>	epl	epl	epl	3
<i>Streblotrichum convolutum</i>	epg	-	epg	2
<i>Syntrichia papillosa</i>	epph	epph	epph	2
<i>Syntrichia ruralis</i>	epl	epl	epl	3
<i>Syntrichia virescens</i>	-	epph	epph	2
<i>Tortula acaulon</i>	epg	epg	-	1
<i>Tortula muralis</i>	epl	epl	epl	3

In a nearby urban woodland Horský park (Fig. 1B), Godovičová (2019) documented 57 bryophyte species (six liverworts and 51 mosses). When comparing species composition between Calvary Hill and Horský park, the Jaccard similarity coefficient was low ($J_c = 0.426$), probably reflecting differences in habitat structure and environmental conditions. The area size of Horský park is larger with more diverse substrates, and contains several water sources contributing to increased humidity, thereby supporting a greater species richness.

Historical sources highlight substantial changes in the vegetation of Calvary Hill from the 18th century to the present (Ptačovský 1959, Letz 2000, Reháčková et al. 2007). Visual comparison with historical illustrations (Fig. 2A–C) supports this shift. Lumnitzer (1791) provided the earliest floristic records, listing 47 vascular plant species, and describing the site as dry, xerothermic grasslands and pastures on acidic substrates, interspersed with shrubs and cultivated fields (Letz 2000, Reháčková et al. 2007). Ptačovský (1959) later characterized the area as hosting primarily steppe communities.

Historical bryological records further confirm this open habitat character. In the first floras from Bratislava, neither Lumnitzer (1791) nor Endlicher (1830) reported bryophytes from Calvary Hill. The first bryophyte records were published by Bäumler (1884), who listed 11 mosses, later summarized by Györfy (1908). Most of these species preferred dry, sun-exposed habitats with low vascular plant competition, such as *Acaulon muticum*, *Aloina ambigua*, *Brachythecium albicans*, *Encalypta streptocarpa*, *Microbryum curvicolium*, and *Tortula protobryoides*. Of these, only *Syntrichia virescens*, a facultative epiphyte, was confirmed during the present survey. Other historical species are now rare or locally extinct in Bratislava, e.g., *Aloina ambigua*, *Microbryum curvicolium*, *Ephemerum serratum*, *Campylophyllopsis calcarea*, and *Rhytidiadelphus triquetrus*.

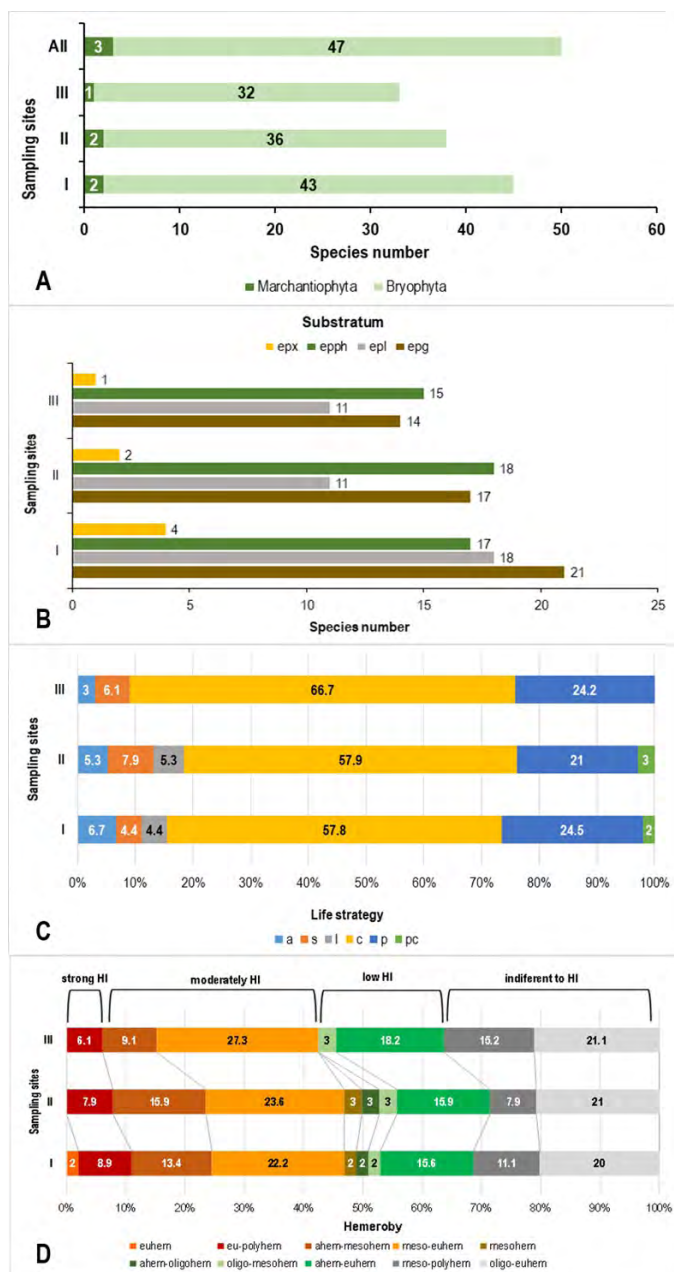


Fig. 4. Representation of substrates and selected biological traits of bryophytes on Calvary Hill. Sampling sites: I - slopes above Pražská street, II - remains of oak stand, III - the top part of Calvary Hill. **A.** Number of species. **B.** Number of species in substratum categories; epg – epigeic species, epl – epilithes, epph – epiphytes, epx – epixylic species. **C.** Percentage of bryophyte life strategies; a – annual species, c – colonist, p – perennial species, pc – competitive perennials, s – short lived shuttle, l – long lived shuttle. **D.** Percentage of bryophyte species in degrees of hemeroby; HI – human impact; ahem – ahemerobic, oligohem – oligohemerobic, meso/mesohem – mesohemerobic, eu/euhem – euhemerobic, polyhem – polyhemerobic.

In terms of substrate preference (Fig. 4B), no statistically significant differences were observed among the three study sites. SS I supported the highest number of epigeic species, mainly along woodland paths and soil gaps in the paved areas of the Stations of the Cross. It also hosted the highest number of epilithic mosses due to the presence of stone and concrete structures and debris slopes. SS II showed the highest abundance of epiphytes, primarily growing on oaks, ashes, and maples. SS III, with the lowest total bryophyte richness, had relatively well-developed epiphyte assemblages on ashes; however, future preservation of species composition and abundance remain uncertain due to tree stands thinning associated with ongoing restoration works. Epixylic species were scarce across all SSs, likely due to the limited availability of suitable substrates and the predominantly dry and warm microclimatic conditions (Kropik et al. 2021).

Within the life strategies (Fig. 4C), colonists (58% to 67%) and perennials (26% to 24%) were most frequently represented. These include the majority of epiphytes and epilithic species, as well as species preferring stable forest environments. Annual species (3% to 6.7%) and shuttles occurred only rarely (4.4% to 7.9%).

The intensity of anthropogenic impact (Fig. 4D) was relatively high in terms of species composition, as almost half of the species (42% to 47%) tolerated moderate to high HI. Approximately 1/3 of the species were indifferent to HI, while 21% to 25% of bryophytes required low HI.

Only 8% of the recorded bryophytes displayed a strong affinity to forest habitats (Fig. 5A). The majority (56%) were species found in both forested and open habitats, while 36% preferred open landscapes. This distribution is probably shaped by the historical conditions of the locality – mainly open, sun-exposed habitats – which still influence current species composition.

The differences in ecological conditions in individual SS based on EIV were not significantly different. On Calvary Hill, semi-photophilous to semi-shade-tolerant,

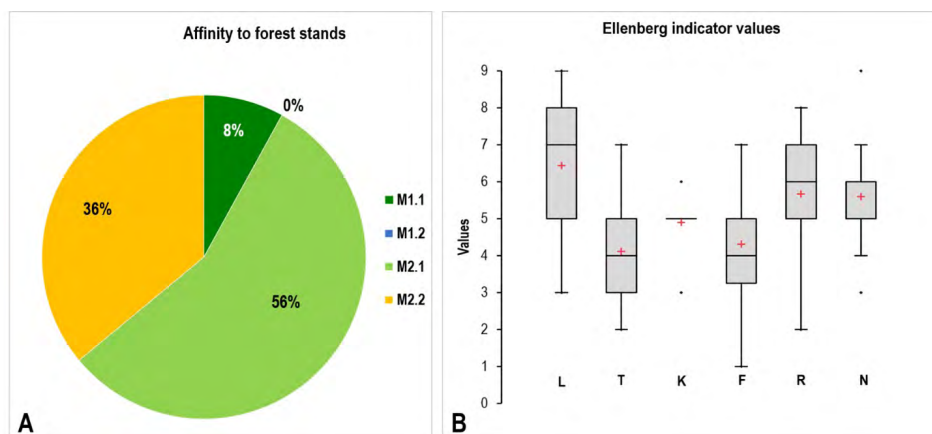


Fig. 5. A: Percentage of bryophyte species in individual categories of forest affinity. M1.1 – largely restricted to closed forest; M1.2 – prefers forest edges and in clearings; M2.1 – occurs in forests as well as in open land; M2.2 – may occur in forests, but prefers open land. **B: Ellenberg indicator values (EIV) for bryophytes observed on Calvary Hill.** L – light, T – temperature, K – continentality, F – moisture, R – reaction, N – nutrients. The box – interquartile range, the whiskers – range of the data, the bold horizontal line in each box – median value, the cross – mean value.

moderately thermophilous, and weakly hygrophilous to xerophilic species dominated (Fig. 5B). Most of them grew on neutral, slightly calcareous to moderately acidic substrates, tolerating medium to slightly higher nutrient content. In terms of continentality, weakly suboceanic to weakly subcontinental bryophytes prevailed (Fig. 5).

Urban woodlands and their fragments are generally subject to intense anthropogenic pressure, resulting in species homogenization and dominance of urban-tolerant taxa (Mežaka et al. 2018). Despite this, such habitats make an essential contribution to urban biodiversity and serve as retention places for various forest species and communities (Širka et al. 2022; Segarra-Moragues, Puche 2024). Conservation efforts should prioritize the protection of existing localities, the preservation of mature trees, the mitigation of fragmentation, and the creation of biocorridors to support species dispersal and long-term persistence (Alvey 2006).

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Abstrakt

Táto štúdia predstavuje prvý bryologický prieskum fragmentu lesa Kalvársky vrch, nachádzajúceho sa v mestskej časti Staré Mesto v Bratislave (Slovensko). Celkovo bolo zaznamenaných 50 druhov machorastov, vrátane 3 pečeňoviek a 47 machov. Jeden druh, *Rhynchostegium rotundifolium* (EN), je zaradený v Červenom zozname machorastov Slovenska. V bryoflóre machorastov dominovali apofytické a urbano-tolerantné druhy (42 % až 47 %), zatiaľ čo druhy viazané na lesné prostredie (8 %) sa vyskytovali zriedkavo. Loaklita bola rozdelená na tri odberné miesta (SS). Najvyššia druhová bohatosť bola zistená na najväčšom odbernom mieste (SS I), zatiaľ čo prebiehajúce reštaurátorské aktivity negatívne ovplyvnili počet druhov v SS III. Porovnanie s blízkym mestským lesoparkom (Horský park) ukázalo nízku floristickú podobnosť, čo poukazuje na jedinečný charakter Kalvárie. Z hľadiska preferencie substrátu dominovali epigeické (24) a epifytické druhy (21). V rámci životných stratégií boli najčastejšie zastúpení kolonisti (58 % – 67 %) a trváce druhy (26 % – 24 %). Intenzita antropogénneho vplyvu (HI) bola relatívne vysoká, keďže takmer polovica druhov tolerovala stredný až vysoký vplyv. Napriek urbanizačnému tlaku predstavuje Kalvársky vrch významný zdroj biodiverzity v Bratislave, poukazujúc tým na význam ochrany malých zvyškov lesov v mestskom prostredí.

Kľúčové slová: machy, pečeňovky, ekológia urbánneho prostredia, lesné fragmenty, biodiverzita, stredná Európa

SEVEROAMERICKÉ ASTRY (*SYMPHYOTRICHUM* SPP.) V STREDNEJ EURÓPE: URČOVANIE A TAXONOMICKÉ VÝZVY

NORTH AMERICAN ASTERS (*SYMPHYOTRICHUM* SPP.) IN CENTRAL EUROPE: IDENTIFICATION AND TAXONOMIC CHALLENGES

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Abstract

The genus *Symphyotrichum* Nees (Asteraceae) comprises more than one hundred species, predominantly of North American origin, some of which have been introduced into Europe as ornamental plants. In Central Europe, *S. lanceolatum* and its hybrids with *S. novi-belgii* have become naturalized. As a result of introgression, these taxa show considerable morphological variability, which poses serious difficulties in their identification. The aim of this study was to evaluate both historical and current aspects of the occurrence of North American asters in the Pannonian Basin and to clarify the taxonomic problems associated with their delimitation. We analyzed data from the literature, herbarium specimens and field observations, focusing on morphological traits useful for the diagnosis of species and hybrids. Our results confirm that traditional diagnostic characters, such as leaf auriculation, are unreliable in the presence of polyploid cytotypes. Therefore, we propose a set of diagnostic traits based on capitulum morphology that allow the differentiation of selected taxa, in particular *S. lanceolatum*, *S. novi-belgii* and their introgressive hybrids (*S.* × *salignum*, *S.* × *versicolor*). Special attention is paid to spontaneous hybrids and cultivars, which require further taxonomic revision. Our findings provide a practical guide for the identification of naturalized *Symphyotrichum* populations in Central Europe and contribute to a better understanding of their morphological and ecological diversity.

Kľúčové slová: nepôvodné rastliny, *Aster novi-belgii* agg., Asteraceae

Úvod

Rod *Symphyotrichum* Nees (Asteraceae) zahŕňa približne 100 druhov, rozšírených prevažne v Severnej Amerike (Fenneman 2019). Do Európy bolo zavlečených dvanásť druhov tohto rodu ako okrasných rastlín, pričom niektoré z nich vykazujú invázne správanie (Tutin et al. 1976; Jedlička, Prach 2006). Z týchto druhov sú pre strednú Európu najvýznamnejšie dva druhy, *S. novi-belgii* (L.) G. L. Nesom a *S. lanceolatum* (Willd.) G. L. Nesom, vrátane ich krížencov (Hrabovský et al. 2025).

Oba zmienené druhy sa v Panónskej panve pestovali ako okrasné trvalky od začiatku

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19. storočia (Endlicher 1830, Priszter 1997). Avšak druh *S. novi-belgii* bol postupne vytlačený jeho záhradnými hybridmi, nazývanými *S. × salignum* Willd., ktoré sa od konca 19. storočia do polovice 20. storočia šírili v Európe (Hrabovský et al. 2025). Zároveň sa začali objavovať nové spontánne introgresívne hybridy, v tej dobe ešte považované za druhy rodu *Aster*, napríklad *A. pesthinensis* DC. a *A. hybridus* Krause (Nees von Esenbeck 1833, De Candolle 1864, Krause 1905).

Hybrid *S. × salignum* bol v 20. storočí postupne nahradený novou generáciou introgresívnych hybridov medzi druhom *S. novi-belgii* a inými severoamerickými astrami (predpokladalo sa, že išlo napr. o *S. laevis* (L.) Á. Löve et D. Löve) (Hoffman 1996). Tieto hybridné kultivary, niekedy nazývané *S. × versicolor* (Willd.) G. L. Nesom, sú v súčasnosti naturalizované v horských oblastiach obklopujúcich Panónsku panvu (Hrabovský et al. 2025).

Od druhej polovice 20. storočia sa začal v Európe šíriť oktaploidný cytotyp *S. lanceolatum* ($2n = 64$) (Hrabovský et al. 2025), ktorý bol pestovaný pre okrasu v záhradách viacerých krajín, napr. v Nemecku už pred rokom 1810 (Mears 1978), vo Francúzsku okolo roku 1815 (Tison, de Foucault 2014), v susednom Maďarsku pred rokom 1825 (Priszter 1997) a v Belgicku v roku 1835 (Verloove 2006). Nie je presne známe, kedy bol tento cytotyp introdukovaný do stredoeurópskych krajín, ako je Česká republika (Pyšek et al. 2002), Rakúsko (Essl, Rabitsch 2002) alebo Slovensko (Fehér 2008). Naše predošlé výskumy naznačujú, že to mohlo byť približne pred rokom 1917 z územia povodia Moravy (Michalová et al. 2024).

V súčasnosti sa v strednej Európe vyskytujú okrem vyššie uvedených taxónov nové generácie hybridov vstupujúcich do ďalšieho kríženia s naturalizovanými populáciami (Hrabovský et al. 2025). Populácie tak vykazujú značnú morfológickú variabilitu, často s prekrývajúcimi sa znakmi medzi druhmi, čo spôsobuje problémy pri ich taxonomickej identifikácii (Meinert et al. 2009). Štúdium veľkosti genómu v kombinácii s morfometrickou analýzou sa ukázalo ako jedna z najspoľahlivejších metód na identifikáciu druhov v rode *Symphyotrichum* (Dirkse et al. 2014, Hrabovský et al. 2025).

Cieľom tohto príspevku je objasniť vzťahy medzi taxónmi vyskytujúcimi sa v Panónskej panve a zjednodušiť určovanie naturalizovaných druhov a hybridov na základe morfológických a ekologických znakov populácií.

Materiál a Metódy

Tento článok vychádza z našich predošlých výskumov, kde sme hodnotili variabilitu v počte chromozómov a veľkosti DNA na konkrétnych jedincoch, ktoré sme z pôvodných lokalít (z rôznych častí strednej Európy) presadili a pestovali pri rovnakých kultivačných podmienkach (Michalová et al. 2024, Hrabovský et al. 2025). Pri týchto jedincoch bola hodnotená aj molekulárna variabilita, ktorá je predmetom pripravovaného článku, a ktorá len potvrdila predpoklady založené na morfológických znakoch o neustále prebiehajúcej hybridizácii amerických astier, vyslovené v diskusii našej poslednej publikácie (Hrabovský et al. 2025). Tieto jedince so známou karyológiou a pôvodom sme morfológicky analyzovali za účelom správnej identifikácie taxónov, ktoré sa na Slovensku a v okolitých štátoch vyskytujú voľne v prírode alebo sú pestované.

Medzi tieto jedince boli zaradené aj také, ktoré sme získali na vedecký výskum priamo z kanadských a amerických nažiek), aby sme mali porovnávací materiál geneticky čistých pôvodných taxónov oproti skúmaným introdukovaným astrám.

Výsledky a diskusia

Flóra Slovenska uvádza šesť naturalizovaných druhov, ktoré sa môžu vyskytovať v strednej Európe, a ďalšie druhy, taxóny a krížence pestované v záhradách (Miháliková et al. 2023). Naše dodatočné výskumy karyológie zodpovedali nevyriešené otázky o výskyte *S. novi-belgii* a *S. × salignum* v strednej Európe a o spontánnom krížení druhu *S. lanceolatum* (Hrabovský et al. 2025). V Európe sa od minulosti po súčasnosť vyskytovali diploidné ($2n = 16$) až oktoploidné druhy ($2n = 64$), ktoré podľa stupňa ploidie analyzujeme v nasledovnom texte.

(1) Medzi diploidné druhy ($2n = 16$), ktoré sa v minulosti v strednej Európe zriedkavo vysádzali, patrí *S. tradescantii* (L.) G. L. Nesom. Dnes sa táto diploidná astra v Európe nevyskytuje. Diploidné až tetraploidné sú aj pestované druhy *S. novae-angliae* (L.) G. L. Nesom, ktorý zriedkavo splanieva (M. Michalová, in verb.), a *S. ericoides* (L.) G. L. Nesom, ktorý sa zriedkavo vysádza v botanických záhradách (Obr. 1a).

(2) Tetraploidné astrы ($2n = 32$) boli v minulosti v strednej Európe zastúpené európskym hybridom s nedoriešenou taxonómiou *Aster parviflorus* hort. non Nees (Obr. 1b). Európske monografie ho označujú ako nový taxón *S. parviflorum* (Nees) Greuter (Kubát 2019), zatiaľ



Obr. 1. Diploidné a tetraploidné astrы a) *Symphyotrichum ericoides*, b) hybrid *Symphyotrichum* ‚Parviflorum‘

Fig. 1. Diploid and tetraploid asters a) *Symphyotrichum ericoides*, b) *Symphyotrichum* ‚Parviflorum‘ hybrid

čo v Amerike je druh *S. parviflorum* (Nees) Greuter stotožňovaný so *S. expansum* (Poepp. ex Spreng.) G. L. Nesom (Powell, Worthington 2018). Tento taxón (*S. parviflorum*) sa v súčasnosti vyskytuje už len v Západnej Európe (Dirkse et al. 2014 ako *S. ontarionis* (Wiegand) non G. L. Nesom). Predpokladá sa, že ide o introgresívny hybrid medzi *S. lanceolatum* a inými druhmi (Hrabovský et al. 2025). Tento taxonomicky nevyriešený hybrid, pre ktorý navrhujeme provizórne označenie *Symphotrichum* „Parviflorum“, má veľmi drobné úbory široké do 3 mm (pri herbárových položkách do 7 mm) a listy na rubovej strane chlpaté, čím sa nápadne podobá na *S. ontarionis*. Na rozdiel od tohto druhu je hybrid takmer úplne sterilný (Kubát 2019).

(3) Medzi hexaploidné ($2n = 48$) druhy patrí väčšina veľkouborových a vo sfarbení lúča farebne premenlivých astier. Tieto záhradné hybridy a kultivary sú označované obchodníckym menom *Aster novi-belgii* non L. Pôvodný druh *S. novi-belgii* sa v strednej Európe nevyskytuje (s výnimkou súkromných zbierok). Jedince mylne označované za tento druh sú hybridmi (Miháliková et al. 2023). *S. novi-belgii* možno jednoznačne rozpoznať podľa odstávajúcich zelených zákrovných listov (Obr. 2a). Zámery sú možné s hexaploidnými krížencami, napr. so *S. × salignum* (Obr. 2b), v minulosti hojne vysádzaným taxónom, no v súčasnosti veľmi zriedkavým. Ide o kríženca medzi *S. lanceolatum* a *S. novi-belgii* (Jones, Hiepkó 1981), ktorý sa ale introgresívne križil so svojimi rodičmi, preto vykazoval vysokú morfológickú variabilitu. V súčasnosti, keď sa hexaploidný cytotyp *S. lanceolatum* v strednej Európe už nevyskytuje, je tento taxón ovplyvnený tokom génov z iných hexaploidov, a pôvodné splanené jedince *S. × salignum* dožívajú na okraji areálu Panónske panvy. Hybrid *S. × salignum* bol v 20. storočí nahradený taxónom *S. × versicolor* (Obr. 3a), ktorý predstavuje novú generáciu introgresívnych hybridov medzi *S. novi-belgii* a inými druhmi. Predpokladá sa, že domnelým rodičovským taxónom mohol byť pravdepodobne druh *S. laeve* (Hoffman 1996), ktorý je ľahko odlíšiteľný vďaka oinovateným listom a ktorý sa dnes v Európe vyskytuje výlučne v súkromných zbierkach (Obr. 3b). Naše predbežné výsledky fylogenetických markerov však naznačujú, že tento taxón (*S. × versicolor*) vznikol krížením medzi *S. × salignum* a *S. praealtum* (Poir.) G. L. Nesom. V súčasnosti je naturalizovaný hlavne v horských oblastiach študovaného regiónu (Michalová et al. 2024, Hrabovský et al. 2025).

Zvláštnu skupinu hexaploidných astier predstavuje skupina hybridov, ktoré mali záhradnícke označenie „Dumosus“ (Hettterscheid, van den Berg 1996). Krause (1905) predpokladal, že vznikli zo skupiny hybridov „Parviflorus“. Tie sa ale ukázali byť tetraploidné (Hrabovský et al. 2025). Podľa našich predbežných výsledkov sa jedná o viacdruhovú skupinu hybridov medzi *S. novi-belgii*, *S. praealtum* a *S. lanceolatum*, prípadne inými druhmi. Možno teda predpokladať, že ide o skupinu kultivarov vyšľachtených zo *S. × versicolor*, a čím viac morfológických znakov *S. lanceolatum* prevláda, tým sú astry kričkovitejšie. Doposiaľ česká aj slovenská literatúra (Kubát 2019, Miháliková et al. 2023) uvádzala, že tieto hexaploidné krížence sú azda hybridom medzi hexaploidným *S. novi-belgii* a nezávislým diploidným až tetraploidným druhom *S. dumosum* (L.) G. L. Nesom, ktorý sa v minulosti síce v Európe pestoval, ale dnes sa už nevyskytuje (Hrabovský et al. 2025). Podľa našich predbežných analýz sa tieto kultivary križia s divorastúcimi astrami zo skupiny *S. × versicolor*.



Obr. 2. Hexaploidné astry 1 a) *Symphyotrichum novi-belgii*, b) hybrid *Symphyotrichum* × *salignum*

Fig. 2. Hexaploid asters 1 a) *Symphyotrichum novi-belgii*, b) *Symphyotrichum* × *salignum* hybrid



Obr. 3. Hexaploidné astry 2 a) hybrid *Symphyotrichum* × *versicolor*, b) *Symphyotrichum laeve*

Fig. 3. Hexaploid asters 2 a) *Symphyotrichum* × *versicolor* hybrid, b) *Symphyotrichum laeve*

(4) Heptaploidné astry ($2n = 56$) sú spontánne krížence medzi oktaploidným *S. lanceolatum* ($2n = 64$) a akýmkoľvek hexaploidnými astrami ($2n = 48$) uvedenými vyššie. Pre ich nesmiernu morfológickú variabilitu sú zamiňané hlavne so *S. lanceolatum*, *S. novi-belgii*, *S. praealtum*, *S. × salignum* a *S. × versicolor* (Hrabovský et al. 2025). Neexistuje takmer žiadna cytologicky čistá populácia, kde by sa heptaploidy nevyskytovali (Hrabovský et al. 2025). To viedlo v minulosti k zmätkom v určovaní a k zavedeniu súborného druhu *Aster novi-belgii* agg. Pokiaľ sú heptaploidy prítomné v populáciách *S. lanceolatum*, dajú sa spoznať podľa oneskoreného kvitnutia, menšieho počtu úborov, väčšej náchylnosti na hubové ochorenia, ale aj podľa odlišného tvaru zákrovov v porovnaní s okolitými rastlinami (Obr. 4). Niektoré zákrovy heptaploidných jedincov sa nápadne ponášajú na zákrovy *S. praealtum* (Obr. 4a), *S. × salignum* (Obr. 4b–c) alebo *S. novi-belgii* (Obr. 4d).

Heptaploidné krížence sú ťažšie rozlíšiteľné v hexaploidných populáciách, keďže veľkosťou úborov a lúčovitých kvetov sa zásadne neodlišujú od iných hexaploidov. Majú však často škridlicovito usporiadané listene zákrovu (Obr. 5a), čo je znak typický pre *S. lanceolatum* (Obr. 6). Práve toto usporiadanie mohlo viesť k mylnej domienke, že jeden z rodičov je *S. laeve*, ktorý má veľmi podobne zákrovné listene (porov. Obr. 3b), alebo pri čiastočne škridlicovitom usporiadaní (Obr. 5b) k zámenám so *S. × salignum* (porov. Obr. 2b).



Obr. 4. Heptaploidné astry 1 a) – d) hybridy *Symphyotrichum lanceolatum*

Fig. 4. Heptaploid asters 1 a) – d) *Symphyotrichum lanceolatum* hybrids



Obr. 5. Heptaploidné astry 2 a) – b) hybridy *Symphyotrichum lanceolatum*

Fig. 5. Heptaploid asters 2 a) – b) *Symphyotrichum lanceolatum* hybrids

(5) Oktoploidné astry ($2n = 64$) sú reprezentované najrozšírenejším druhom *S. lanceolatum*, ktorý jediný zo všetkých severoamerických druhov astier na území strednej Európy vykazuje invázne správanie (Michalová et al. 2024). Tento druh sa vyskytuje prevažne v nížinách a v pahorkatinách a je ľahko rozpoznateľný; má menšie úbory aj lúčovité kvety a škridlicovito usporiadané listene zákrovu (Obr. 6).



Obr. 6. Oktoploidné astry 2 a) – c) *Symphyotrichum lanceolatum*

Fig. 6. Octoploid asters 2 a) – c) *Symphyotrichum lanceolatum*

Záver

V tomto príspevku sme zodpovedali taxonomické poznámky uvedené pri druhoch *S. lanceolatum*, *S. novi-belgii* a pri niektorých ich krížencoch v diele *Flóra Slovenska* (Miháliková et al. 2023). Naďalej ostáva otáznе rozdeľovanie druhov podľa kritéria tuhosti a uškatosť listov, ktoré je v praxi, hlavne pre prítomnosť heptaploidov, nevyužiteľné. Na rozlišovanie druhov a hybridov súborného druhu *Aster novi-belgii* agg. je vhodné riadiť sa nasledovnými znakmi:

- *Symphyotrichum novi-belgii* – listy jemné, na báze objímavé (uškaté), úbory stredne veľké (zákrov s priemerom 6 – 9 mm), listene zákrovu listovité, odstávajúce, lúčovité kvety väčšinou svetlofialovo sfarbené; druh sa na Slovensku voľne nevyskytuje.
- *Symphyotrichum* × *salignum* – listy jemné, na báze objímavé, úbory malé až stredne veľké (zákrov s priemerom 4 – 9 mm), listene zákrovu čiastočne odstávajúce, lúčovité kvety väčšinou bielo bledofialkasté; kríženec je na Slovensku takmer vyhynutý.
- *Symphyotrichum* × *versicolor* – listy mäsité, na báze objímavé (uškaté), úbory stredne veľké až veľké (zákrov s priemerom 7 – 15 mm), listene zákrovu pritlačené, škridlicovité až rovnako dlhé, lúčovité kvety väčšinou farebné; kríženec je na Slovensku bežný v podhorskom až horskom stupni.
- Kultivary *Symphyotrichum* – listy mäsité, na báze objímavé (uškaté), pod súkvetím nápadne zmenšené, úbory stredne veľké až veľké (zákrov s priemerom 7 – 15 mm), listene zákrovu pritlačené, rovnako dlhé, lúčovité kvety väčšinou farebné; na Slovensku pestované a vyžadujú taxonomickú revíziu.
- Hybridy *Symphyotrichum lanceolatum* – listy jemné až mäsité, na báze sediace až poloobjímavé, úbory stredne veľké (zákrov s priemerom 4 – 9 mm), listene zákrovu pritlačené alebo čiastočne odstávajúce, rovnako dlhé, lúčovité kvety

väčšinou bielo bledofialkasté; krížence sú na Slovensku hojné a vyžadujú taxonomickú revíziu.

- *Symphyotrichum lanceolatum* – listy jemné, na báze sediace až poloobjímavé, úbory malé až stredne veľké (zákrov s priemerom 3 – 7 mm), listene zákrovu škridlicovité, pritlačené, nerovnako dlhé, lúčovité kvety väčšinou biele alebo bledofialkasté; druh je na Slovensku hojný hlavne v nížinách a pahorkatinách.

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Abstrakt

Rod *Symphyotrichum* Nees (Asteraceae) zahŕňa viac ako sto druhov, prevažne severoamerického pôvodu, z ktorých viaceré boli introdukované do Európy ako okrasné rastliny. V strednej Európe sa naturalizovali najmä *S. lanceolatum* a jeho hybridy so *S. novi-belgii*, ktoré v dôsledku introgresie vykazujú výraznú morfológickú variabilitu a spôsobujú značné ťažkosti pri určovaní. Cieľom tejto práce bolo zhodnotiť historické aj súčasné aspekty výskytu severoamerických astrií v Panónskej panve a objasniť taxonomické problémy spojené s ich rozlišovaním. Analyzovali sme údaje z literatúry, herbárových dokladov a terénnych pozorovaní, so zameraním na morfológické znaky využiteľné v diagnostike druhov a hybridov. Výsledky potvrdzujú, že tradičné určovacie znaky ako je uškatosť listov sú vzhľadom na prítomnosť polyploidných cytotypov málo spoľahlivé. Navrhujeme preto súbor diagnostických znakov na základe morfológie úborov umožňujúcich rozlišovanie vybraných taxónov, najmä *S. lanceolatum*, *S. novi-belgii* a ich introgresívnych hybridov (*S.* × *salignum*, *S.* × *versicolor*). Osobitnú pozornosť venujeme spontánnym hybridom a kultivarom, ktoré si vyžadujú taxonomickú revíziu. Naše výsledky poskytujú praktický návod pre určovanie naturalizovaných populácií rodu *Symphyotrichum* v strednej Európe a prispievajú k lepšiemu pochopeniu ich morfologickej a ekologickej diverzity.

Kľúčové slová: alien plants, *Aster novi-belgii* agg., Asteraceae

SOIL CYANOBACTERIA AND ALGAE FROM THE CARPET MEADOW, TARA NATIONAL PARK, SERBIA

PÔDNE CYANOBAKTÉRIE A RIASY KOBERCOVEJ LÚKY,
NÁRODNÝ PARK TARA, SRBSKO

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Abstract

This study characterizes the species composition of cyanobacteria and algae in the soil of the Carpet Meadow in Tara National Park, Serbia, providing the first systematic survey of terrestrial microflora at this site. A total of 45 taxa were identified, belonging to 8 genera of cyanobacteria and 24 genera of algae. The soil communities were dominated primarily by taxa with broad ecological tolerance and by species adapted to oligotrophic to mesotrophic and slightly acidic conditions.

Key words: cyanobacteria, forest soil, peat soil, terrestrial algae.

Introduction

Tara National Park is one of the five national parks in Serbia, located in the western part of the country within the Tara Mountain massif of the Inner Dinarides and the Serbian Vlach Mountains. The park features rugged limestone terrain, with peaks reaching up to 1600 m a.s.l., deep canyons and gorges, and extensive forest cover (approximately 80% of the park's area). Over 1,100 plant species have been recorded, accounting for nearly one-third of Serbia's flora. The forests predominantly consist of mixed coniferous and deciduous stands, including spruce, fir, and beech, interspersed with meadows, pastures, and peat bogs. The protected status of the area supports numerous rare, relict, endangered, and endemic plant species, including the endemic relict Serbian spruce (*Picea omorica*) (Tara National Park 2018).

The Carpet Meadow (Tepih Livada) sampling site (Fig. 1–2) is located within the Crveni Potok Nature Reserve in the central part of the park at approximately 1,080 m a.s.l. It harbors one of the region's most unique and ecologically significant habitats – a peat bog. This 23-hectare area has developed on impermeable bedrock under cold and humid climatic conditions, promoting waterlogging and peat formation through the accumulation of undecomposed plant material and the presence of moss communities,

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primarily *Sphagnum* species, since the last Ice Age (Tourist Organisation “Tara-Drina”, 2024). The area is called Carpet Meadow due to its soft, springy peat surface, which resembles a carpet. Because of its ecological sensitivity, high conservation value, and substantial visitors pressure, access to the peat surface is now restricted (Tara.rs, n.d.).

Numerous botanical and paleobiological studies have been conducted in Tara National Park. The vegetation communities of meadows, pastures, and peat bogs were reviewed by Jovanović (1989, 1991). Paleobiological research based on pollen analyses was published by Finsinger et al. (2017) and others. Studies on the species richness of fungi, bryophytes, and lichens in Tara National Park have been carried out by Papp, Sabovljević (2002), Savić, Tibell (2006), Savić et al. (2006), Tibell, Savić (2008), Sabovljević et al. (2023), Sabovljević et al. (2025), and others.

In Serbia, numerous algological studies have been conducted and continue to be carried out. Algae from shallow and small water bodies were analyzed by Trbojević, Predojević (2022). Research on phototrophic organisms and chemotrophic fungi in selected caves was presented by Popović et al. (2017), while the diversity of phototrophs in thermomineral springs was studied by Milicević et al. (2025). Investigations of red algae in river ecosystems have been conducted since the late 20th century (e.g., Mitrović et al. 2021, Rakonjac, Simić 2023). Recent studies on benthic, epiphytic, and planktonic diatoms include work by Vidaković et al. (2016), while an overview of charophyte research in Serbia was provided by Blaženić (2014). The diversity of desmids from the water of Tara Mountain peat bogs was first described by Milovanović (1962). Extensive recent data on desmid diversity from both Tara National Park and other regions of Serbia have been published by Stamenković et al. (2008), Fužinato et al. (2011a, 2011b, 2012, 2013), and Šovran et al. (2013, 2022), and others.

Despite extensive research efforts, no publications addressing the diversity of soil cyanobacteria and algae at the Carpet Meadow site have been found, except of those focusing on desmids. The diversity of phototrophic cyanobacteria and algae in this locality remains largely unknown. Jafari et al. (2022) reported that the diversity and taxonomy of green soil microalgae in Serbia have not yet been studied.

Material and methods

Natural conditions

The Carpet Meadow site (Fig. 1), located at N 43°54'50", E 19°25'11" at an elevation of 1,080 m a.s.l., is situated within the Red Creek (Crveni Potok) Nature Reserve in Tara National Park, Serbia. This area represents a unique peatland habitat characterized by consistently high soil moisture and acidic conditions. The originally impermeable subsoil has facilitated the accumulation of organic matter, particularly *Sphagnum* mosses, contributing over time to development of organic peat soil. As this organic matter accumulates and undergoes accelerated humification, it gradually leads to the formation of an alkaline substrate (Tešić et al. 1979). The region's climate is characterized by a mean annual temperature of 8–10°C and average annual precipitation 800–900 mm (Ministry for Environmental Protection 2022).

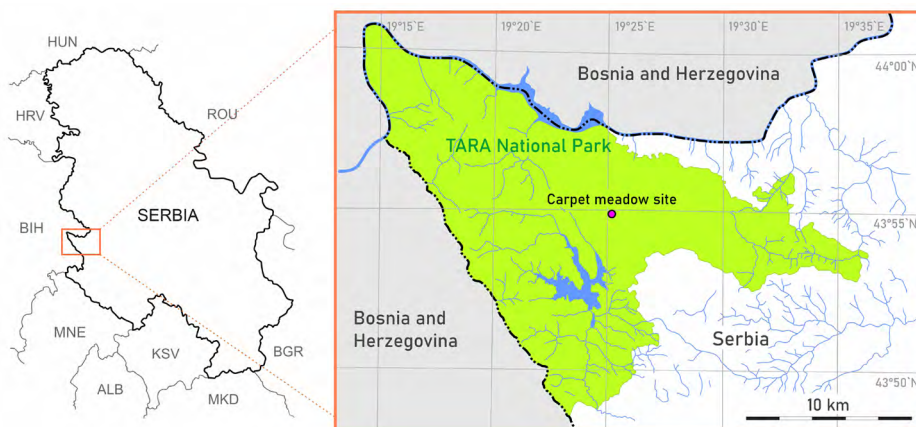


Fig. 1. Location of the sampling site.

Sample collection and processing

In 2014, during a field excursion led by the staff of Tara National Park, a small sample of the upper layer of unvegetated soil was carefully collected from the Carpet Meadow site (Fig. 2) into a sterile container and transported to the Laboratory of Experimental Phycology at Comenius University in Bratislava for detailed analysis.

One portion of the soil sample was examined microscopically, while the second portion was placed in a sterile container with liquid culture medium Z, prepared according to Zehnder (Staub 1961). This sample was cultivated under an irradiance of $50 \mu\text{mol m}^{-2} \text{s}^{-1}$ at a constant temperature of 25°C . The diatoms in the sample were cleaned of organic matter using 30% hydrogen peroxide following standard procedures, and then washed twice with distilled water. The dried material on cover slides was subsequently mounted in Naphrax® mounting medium. Permanent slides and prepared material were deposited at the Laboratory of Experimental Phycology at Comenius University in Bratislava. Light microscopy (LM) observations were performed using a Leica DM 2500 microscope equipped with high-resolution Nomarski DIC optics. Microphotographs were taken with a Leica DFC 290 HD camera and processed using LAS 3.5.0 software.



Fig. 2. Carpet Meadow. A: General view of the sampling site. **B:** Unvegetated soil of the sampling site covered with a layer of cyanobacteria and algae.

Taxonomic identification was performed based on standard literature sources. Cyanobacteria were identified following Komárek, Anagnostidis (1998, 2005), Komárek (2013), and Kaštovský et al. (2018a). Diatoms were identified primarily according to Krammer and Lange-Bertalot (1986, 1988, 1991a, b), Krammer (1992), Lange-Bertalot (1993), as well as Cantonati et al. (2017). Other algal groups were identified using the following references: Hindák (1978), Ettl (1978), Ettl (1983), Ettl, Gärtner (1988), Andreyeva (1998), Lenzenweger (1999), Lenzenweger (2003), Wołowski, Hindák (2005), John et al. (2011), Ettl, Gärtner (2014), and Kaštovský et al. (2018a, b). The classification of cyanobacteria and algae was unified according to Guiry, Guiry (2025).

Results and Discussion

This preliminary survey revealed a relatively diverse assemblage of soil cyanobacteria and algae at the Carpet Meadow site in Tara National Park. A total of 48 taxa were observed, distributed among the following groups: Cyanophyceae (8 species), Bacillariophyceae (21 species), Xanthophyceae (2 species), Chlamydomphyceae (2 species), Chlorophyceae (6 species), Trebouxiophyceae (3 species), Klebsormidiophyceae (1 species), and Zygnematophyceae (2 species). The examined soil sample was predominantly composed of filamentous cyanobacteria, diatoms, and coccoid green algae.

Below is the list of the identified cyanobacterial and algal taxa found in samples collected from Carpet Meadow site:

Cyanophyceae

- Chroococcales: *Chroococcus obliteratus* (Fig. 3A)
- Geitlerinematales: *Geitlerinema splendidum* (Fig. 3A)
- Leptolyngbyales: *Leptolyngbya tenuis* (Fig. 3C)
- Nodosilineales: *Nodosilenia bijugata* (Fig. 3D)
- Nostocales: *Tolypothrix rivularis* (Fig. 3F, G, H)
- Oculatellales: *Drouetiella lurida* (Fig. 3B, H)
- Oscillatoriales: *Oscillatoria tenuis*, *Phormidium kolkwitzii* (Fig. 3E)

Bacillariophyceae

- Bacillariales: *Nitzschia acidoclinata* (Fig. 6F), *N. alpina* (Fig. 6G), *N. palea* (Fig. 6H)
- Cymbellales: *Cymboplectra frequens* (Fig. 6A), *Gomphonema excillissimum* (Fig. 6B), *G. productum* (Fig. 6C)
- Eunotiales: *Eunotia bilunaris* (Fig. 6K), *E. minor* (Fig. 6I), *E. valida* (Fig. 6J)
- Rhabdonematales: *Meridion circulare* (Fig. 6D)
- Naviculales: *Navicula cryptocephala* (Fig. 6E), *N. vulpina*, *Neidium bisulcatum* (Fig. 6M), *Pinnularia gibba* (Fig. 6N), *P. microstauron* (Fig. 6O), *P. nodosa* (Fig. 6P), *P. rupestris* (Fig. 6Q), *P. sinistra* (Fig. 6R), *Sellaphora pseudopupula* (Fig. 6S), *Stauroneis gracilis* (Fig. 6L), *S. kriegei* (Fig. 6T)

Xanthophyceae

- Tribonematales: *Heterococcus* sp., *Tribonema regulare* (Fig. 5E, F)

Chlorophyceae

Oedogoniales: *Oedogonium* sp. sterile (Fig. 4E)

Sphaeropleales: *Bracteacoccus* sp. (Fig. 4A), *Characium* sp. (Fig. 3H), *Coelastrella striolata* (Fig. 4B), *Desmodesmus communis*

Volvocales: *Chlamydomonas* sp. (Fig. 4G), *C. virgata* (Fig. 4F), *Chlorococcum* sp. (Fig. 4C, D)

Trebouxiophyceae

Chlorellales: *Chlorella minutissima* (Fig. 4H), *C. vulgaris* (Fig. 5A)

Trebouxiales: *Myrmecia bisecta* (Fig. 5B)

Klebsormidiophyceae

Klebsormidiales: *Klebsormidium flaccidum* (Fig. 5C)

Zygnematophyceae

Desmidiaceae: *Cosmarium caelatum* (Fig. 5D)

Zygnematales: *Cylindrocystis brebissonii*

To the best of our knowledge, no prior data exist on soil algal communities from this locality. Nevertheless, our findings represent an important first step toward understanding the biodiversity of soil cyanobacteria and algae in the area. Despite the limitations of a single sampling event, this study provides a valuable baseline and emphasizes the need for further research into seasonal dynamics, the ecological roles of these organisms in terrestrial habitats, and the monitoring of indicator species or changes in species composition resulting from tourism pressure or climate change.

The examined soil sample contained relatively common or cosmopolitan taxa, such as the cyanobacteria *Chroococcus obliteratus*, *Leptolyngbya lurida*, and *Leptolyngbya tenuis*. The filamentous cyanobacterium *Oscillatoria minor* is less frequently encountered but also globally distributed. On the other hand, *Phormidium kolkwitzii* has been reported only from European sites, particularly from wet peaty soils or *Sphagnum* bogs (Komárek, Anagnostidis 1998, 2005). The cyanobacterium *Nodosilinia bijugata* has been recorded in Russia, Ukraine, and Central Asia (Komárek, Anagnostidis 2005).

The coccoid and filamentous green algae documented in this study are relatively common in freshwater habitats and moist substrates, such as soil or tree bases (Lokhorst 1996, Ettl and Gärtner 2014). The xanthophyte alga *Tribonema regulare* has frequently been observed in slightly acidic waters, peatlands, and marshy meadows (Ettl 1978), which is consistent with the conditions at our sampling site.

The occurrence of desmids such as *Cosmarium caelatum* and *Cylindrocystis brebissonii* is characteristic of montane humid habitats, including acidic peat waters, fens, slope wetlands, or forest and meadow marshes (Lenzenweger 1999, 2003). *Cosmarium caelatum* has been recorded in acidic waters and ponds in Serbia (Fužinato 2012), while *Cylindrocystis brebissonii* was previously recorded within Tara National Park in the water of the Črvene vode peat bog (Šovran et al. 2014). *C. brebissonii* is a cosmopolitan species, occurring from sea level up to the snow line (Fužinato 2012).

Identified diatoms included species with broad ecological tolerances, such as *Eunotia minor*, *E. bilunaris*, *E. valida*, *Navicula cryptocephala*, *Pinnularia sinistra*, and *Stauroneis kriegeri*, which can tolerate higher trophic levels (Lange-Bertalot 1986, 1988, 1991a, b, Krammer 1992, Lange-Bertalot 1993, Cantonati et al. 2017, Stoermer, Smol 1999). Other diatom taxa are more commonly found in oligotrophic to mesotrophic

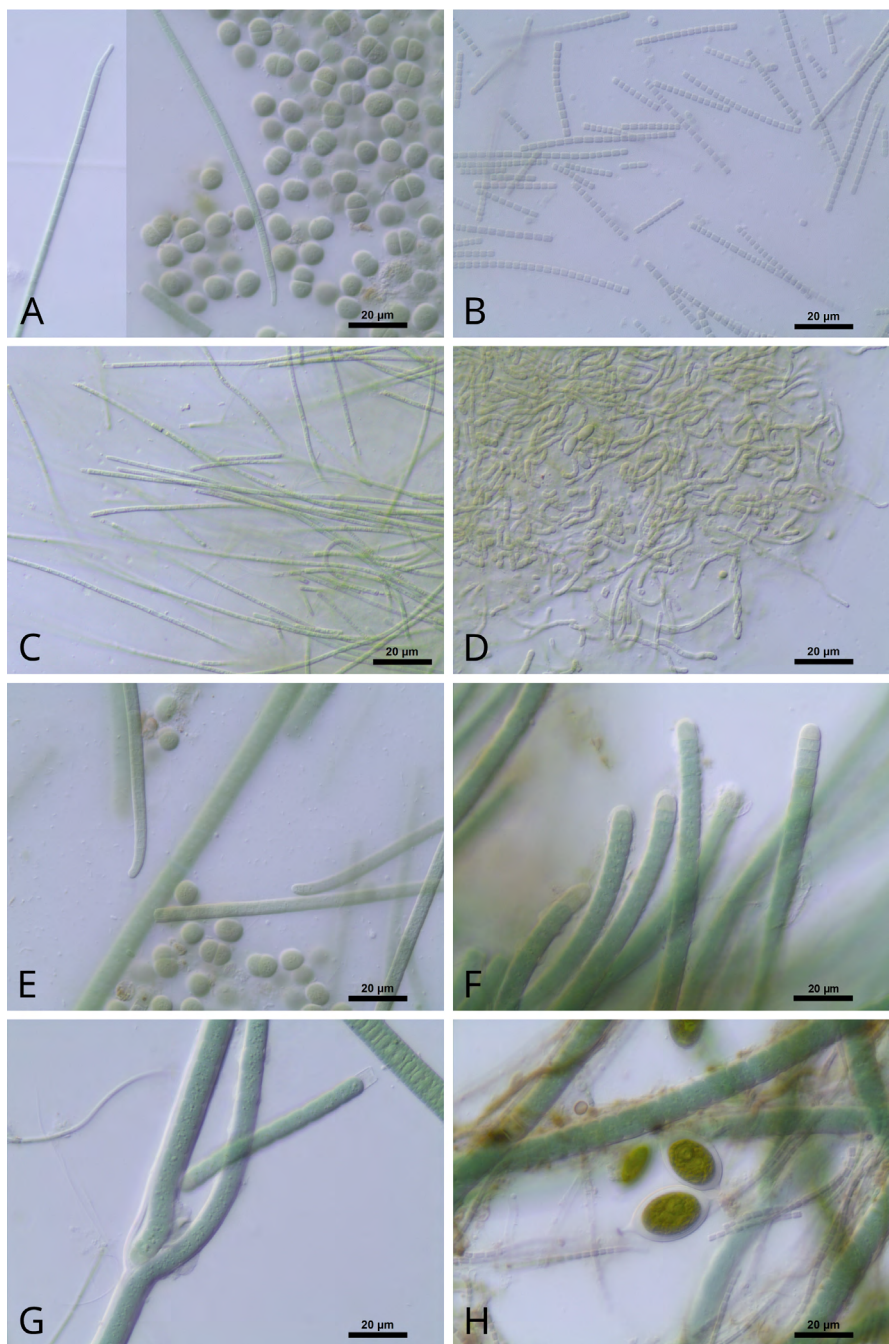


Fig. 3. Light microscopy (LM) microphotographs of the cyanobacterial and algal taxa. **A:** *Chroococcus obliteratus* (the coccal one) and *Geitlerinema splendidum* (the filamentous one). **B:** *Drouetiella lurida*. **C:** *Leptolyngbya tenuis*. **D:** *Nodosilenia bijugata*. **E:** *Phormidium kolkwitzii*. **F:** *Tolypothrix rivularis*. **G:** *T. rivularis*, *Oscillatoria tenuis* (upper right corner). **H:** *Characium* sp., *Drouetiella lurida*, *T. rivularis*.

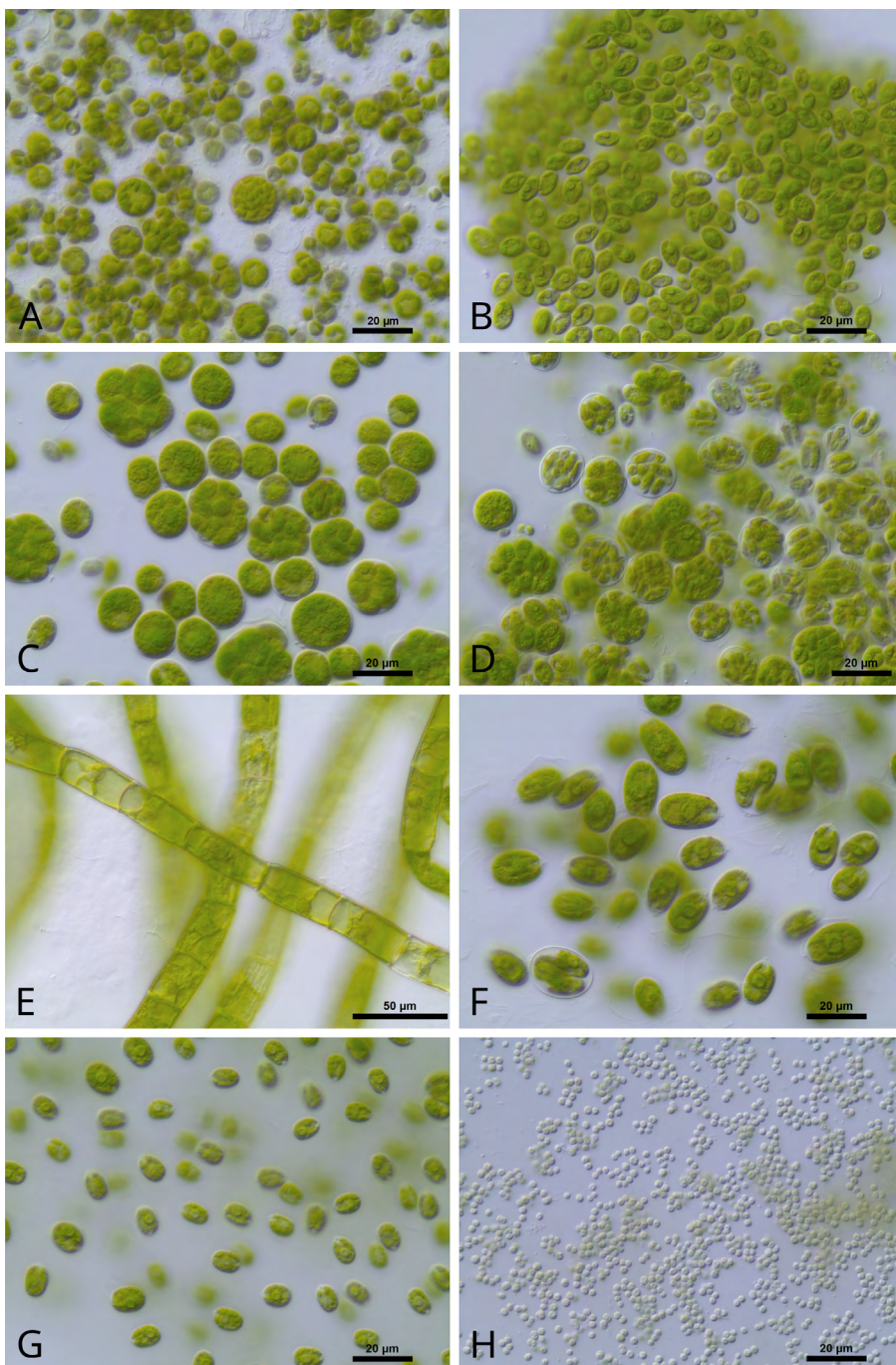


Fig. 4. LM microphotographs of the algal taxa. **A:** *Bracteacoccus* sp. **B:** *Coelastrella striolata*. **C, D:** *Chlorococcum* sp. **E:** *Oedogonium* sp. sterile. **F:** *Chlamydomonas virgata*. **G:** *Chlamydomonas* sp. **H:** *Chlorella minutissima*.

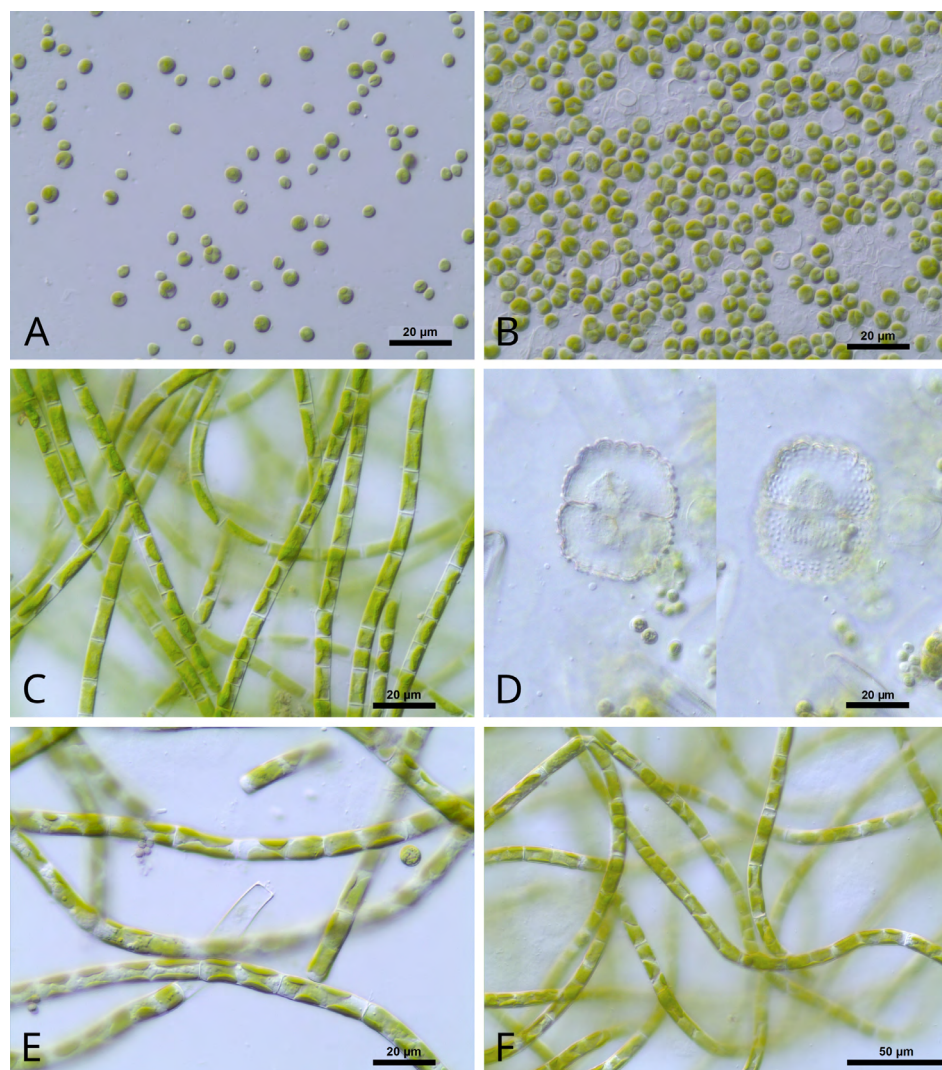


Fig. 5. LM microphotographs of the algal species. **A:** *Chlorella vulgaris*. **B:** *Myrmecia bisecta*. **C:** *Klebsormidium flaccidum*. **D:** *Cosmarium caelatum*. **E, F:** *Tribonema regulare*.

conditions. Acidophilic species dominated the site, known from mildly acidic freshwater habitats (e.g., *Gomphonema exilissimum*, *G. productum*, *Pinnularia gibba*, *Sellaphora pseudopupula*, and *Stauroneis kriegeri*) as well as environments with low to moderate electrolyte content (e.g., *Cymboplectra frequens*, *Navicula vulpina*, *Gomphonema exilissimum*, *G. productum*, *Pinnularia microstauron*, *P. nodosa*, *P. rupestris*, *P. sinistra*, *Sellaphora pseudopupula*, *Stauroneis gracilis*, and *S. kriegeri*). These diatoms are typically associated with habitats featuring submerged vegetation or decaying plant material, consistent with our sampling site.

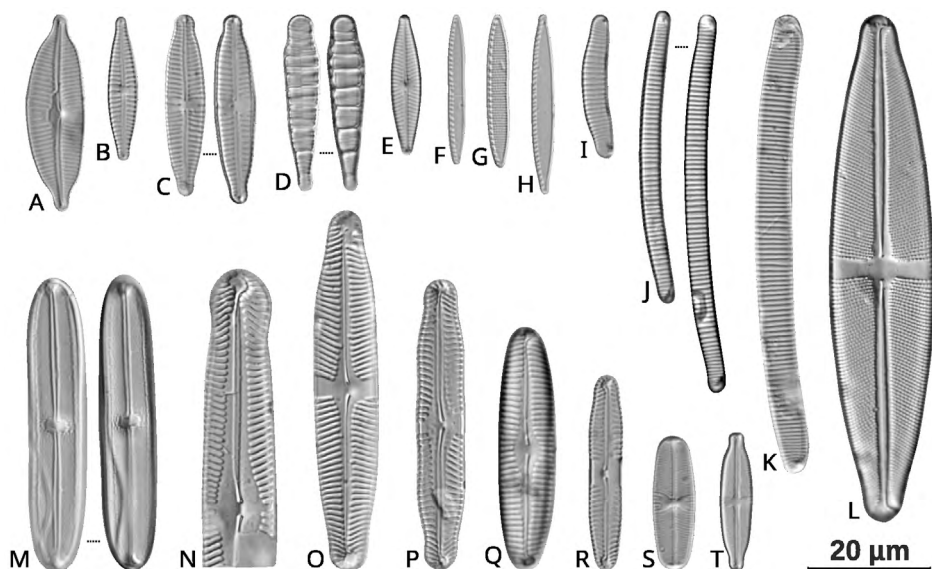


Fig. 6. LM microphotographs of the diatom species. **A:** *Cymboplectra frequens*. **B:** *Gomphonema exillissimum*. **C:** *G. productum*. **D:** *Meridion circulare*. **E:** *Navicula cryptocephala*. **F:** *Nitzschia acidoclinata*. **G:** *N. alpina*. **H:** *N. palea*. **I:** *Eunotia minor*. **J:** *E. valida*. **K:** *E. bilunaris*. **L:** *Stauroneis gracilis*. **M:** *Neidium bisulcatum*. **N:** *Pinnularia gibba*. **O:** *P. microstauron*. **P:** *P. nodosa*. **Q:** *P. rupestris*. **R:** *P. sinistra*. **S:** *Sellaphora pseudopupula*. **T:** *Stauroneis kriegeri*.

Some diatoms, such as *Gomphonema exillissimum*, *Navicula vulpina*, and *Stauroneis kriegeri*, are more commonly found on siliceous substrates, although *N. vulpina* can also colonize decaying plant matter, and *S. kriegeri* can tolerate higher calcium content. *Sellaphora vulpina* is usually associated with siliceous substrates, but Cantonati et al. (2017) suggest that specimens found on calcium-bicarbonate substrates may represent a phenotype of *S. calcicola*. Further research is needed to clarify this hypothesis. Among the noteworthy diatoms recorded, *Gomphonema productum* is considered an indicator species of very high ecological quality.

These preliminary findings provide a baseline for the soil cyanobacterial and algal communities at Carpet Meadow, highlight the need for further research and emphasizing the importance of ongoing monitoring and conservation efforts to preserve this ecologically sensitive peatland habitat.

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Abstrakt

Táto štúdia charakterizuje druhové zloženie cyanobaktérií a rias v pôde lokality Tepih livada (Kobercová lúka, Carpet Meadow) v Národnom parku Tara v Srbsku, pričom ide o prvý systematický prieskum terestrickej mikroflóry na tomto mieste. Celkovo bolo identifikovaných 45 taxónov, ktoré patrili do 8 rodov cyanobaktérií a 24 rodov rias. V pôdnych spoločenstvách dominovali predovšetkým taxóny so širokou ekologickou toleranciou a druhy prispôbené oligotrofným až mezotrofným a mierne kyslým podmienkam.

Kľúčové slová: cyanobaktérie, lesná pôda, rašelinová pôda, pôdne riasy.

ON THE PSEUDONYMOUS SYNTAXONOMICAL APPLICATION OF THE ORDER *ATHYRIO-PICEETALIA* HADAČ 1962

O PSEUDONYMICKOM SYNTAXONOMICKOM POUŽÍVÁNÍ RADU *ATHYRIO-PICEETALIA* HADAČ 1962

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Abstract

Beginning with the well-known vegetation survey *Die Pflanzengesellschaften des Tales „Dolina Siedmich prameňov“ in der Belaer Tatra* of Hadač et coll. on the vegetation of the south-eastern part of the Belianske Tatry Mts (northern Slovakia) and continuing till the present day, most vegetation scientists consistently applied the syntaxonomical order name '*Athyrio-Piceetalia* Hadač 1962' for group of species-rich, usually calcicolous Norway spruce communities. Along with this syntaxon name, the alliance '*Chrysanthemo-Piceion* (Krajina 1933) Březina et Hadač in Hadač 1962' and, less frequently, the alliance '*Oxalido-Piceion* (Krajina 1933) Březina et Hadač in Hadač 1962' have been used as its subordinated syntaxonomical unit. [These two alliance names were proposed as replacement names to '*Chrysanthemion rotundifolii* Krajina 1933' and '*Oxalidion acetosellae* Krajina 1933'.] However, careful revision of original descriptions of these alliance names along with a field examination within the locus classicus surveyed by Krajina (the Mlynická dolina Valley, High Tatras) indicate that their common syntaxonomical application does not correspond to the respective original diagnoses. The current (and long-lasting) phytocoenological approach to these syntaxa names thus represents a demonstrative example of syntaxonomical pseudonyms – '*Chrysanthemo-Piceion* auct. non (Krajina 1933) Březina et Hadač in Hadač 1962' and '*Oxalido-Piceion* auct. non (Krajina 1933) Březina et Hadač in Hadač 1962'. Subsequently, the scientific application of their superordinated order name also constitutes a pseudonym – '*Athyrio-Piceetalia* auct. non Hadač 1962'. Along with a detailed explanation of the factual original characteristics and phytocoenotic content of the alliance names '*Chrysanthemo-Piceion* (Krajina 1933) Březina et Hadač in Hadač 1962' and '*Oxalido-Piceion* (Krajina 1933) Březina et Hadač in Hadač 1962', a brief outline of characteristics and recognition of the syntaxa under consideration is given.

Key words: phytocoenological nomenclature, *Picea abies*, plant communities, syntaxonomy, *Vaccinio-Piceetea*, Western Carpathians, woodland plant communities.

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1. Introduction

The first comprehensive classification of the plant communities of the Central European Norway spruce woodlands (with the Alps included) was presented by J. Braun-Blanquet (in Braun-Blanquet et al. 1939). Within his syntaxonomical division of the class *Vaccinio-Piceetea* Br.-Bl. in Br.-Bl. et al. 1939 (syn. *Piceetea abietis* Klika 1944 nom. corr.¹), Norway spruce woodland plant communities formed only a smaller part of the included syntaxa because this class as well as its subordinated units – order *Vaccinio-Piceetalia* Br.-Bl. in Br.-Bl. et al. 1939 and the alliance *Vaccinio-Piceion* Br.-Bl. ex Br.-Bl. et al. 1939 – contained a broad variety of forest and also non-forest plant communities distributed altitudinally up to the Alpic alpine zone and latitudinally up to the northern border of Fennoscandian taiga zone. Within the latter mentioned syntaxon, coniferous woodland associations were split between a “subalpine suballiance” *Rhododendro-Vaccinienion* Br.-Bl. et al. 1939 and an altitudinally from below adjoining suballiance *Abieti-Piceenion* Br.-Bl. in Br.-Bl. et al. 1939. Besides that, *Picea abies* woodlands of the Harz Mts (northern Germany) were placed outside of these two units – in the largely fennoscandian-baltic-NE European suballiance *Piceion septentrionale* Br.-Bl. et Sissingh in Br.-Bl. et al. 1939 nom. illeg. (Art. 34a).

In fact, the original Braun-Blanquetian zonal separation of Central European *Picea abies* forest plant communities has been frequently disregarded later, and the declared floristic differences represented only one of the floristical-ecological patterns found in the vegetation cover of the Alps primarily. The syntaxonomical content of the “montane” suballiance *Abieti-Piceenion* was not entirely clear (Hadač 1965); furthermore, some syntaxa originally included within *Abieti-Piceenion* would be better classified within the class *Carpino-Fagetea* Jakucs ex Passarge 1968.² Moreover, the Braun-Blanquetian suballiance *Rhododendro-Vaccinienion* comprised not only woodlands but also krummholz and dwarf-shrub non-forest communities. The original approach of Braun-Blanquet et al. (1939) has been more or less abandoned up to the present (cf. already Klika 1944, Hadač 1956; Theurillat et al. 1995 etc).

A little over 20 years later Hadač (1962) published a new concept of classification of natural Norway spruce woodlands based on detailed study within the Tatra Mountains (northern Slovakia) (characterised in detail by Hadač et al. 1969) with the fundamental point of their division defined as the floristic and ecological differences between (1) usually species-poor (“chamaephytic”) communities growing on podzols, (very) strongly acidic soils distributed over nutrient-poor (mostly) siliceous rocks and (2) species-rich (“prevailingly hemicryptophytic”) communities growing on moderately to slightly acidic and neutral soils, inhabiting areas of various carbonate rocks. The first group was placed in the order *Myrtillo-Piceetalia* Hadač 1962 (cf. Art. 14b, however, the correct syntaxon

¹ Under the rules of the recent edition of the phytocoenological Code (Theurillat et al. 2021, Art. 25 vs. Weber et al. 2000, Art. 3m, 25), the name *Vaccinio-Piceetea* is no more evaluated as nomen invalidum (cf. Kučera 2010a, Theurillat in Willner et al. 2015) but as a valid and legitimate name. The Klika’s name (firstly published by Klika 1944) is thus a later heterotypical synonym (Def. X).

² See already Oberdorfer (1957) and earlier (cf. Kučera 2008a); Braun-Blanquet et al. (1939, p. 16–18) [and Brzeg, Rutkowski 2004]] vs. vegetation development documented by Matuszkiewicz (2002, p. 131), Górski (2005), Matuszkiewicz, Kowalska (2007), Maciejewski, Swagrzysk (2011), Świerkosz et al. (2014), Barć et al. (2015), Woziwoda, Kopec (2015), Łukaszewicz et al. (2020); Kučera (2008a, 2023).

name is *Piceetalia abietis* Pawłowski ex Pawłowski et al. 1928), while the second group was separated into the order *Athyrio-Piceetalia* Hadač 1962.

In spite of the fact, that the basic phytocoenological unit (plant association) and more generalised superordinated entities are abstract units (Moravec 1994, Theurillat et al. 2021), and phytocoenology as a science is occasionally criticised (Hédl 2005, etc.),³ syntaxonomical units of the various hierarchical levels resultant from decades of specialised vegetation surveys (and their diverse derivatives, e.g. habitat types as basic classification units for needs of nature conservation), provide valuable application in various scientific disciplines also beyond life sciences, including geography, landscape planning, nature conservation etc., as well as in public education (cf. Braun-Blanquet 1964, Moravec et al. 1994, Ellenberg 1996, Chytrý et al. 2010, Bělóni et al. 2011, W. Matuszkiewicz 2017 (multiple reprints!), Preislerová et al. 2022, Šuvada et al. 2023, Plesník 2004).

The overall as well as specialised characteristics and definitions of studied syntaxa are, however, usually supplemented and refined with the continual cumulation of knowledge, or, should be revised when the conventional use and delimitation would prove problematic. The same applies to the nomenclatural aspect of syntaxonomical studies.

This paper is focused on one of the phytocoenological questions emerging from the confrontation of historical data, their interpretation and specialised field research. Its aim is to deal with the syntaxonomical problems inferred from the difference between the factual floristic and ecological content of the order *Athyrio-Piceetalia* Hadač 1962 as determined by its original diagnosis and the common use of this unit. Firstly, the recognition of the discussed names in European literature is given in order to provide a more comprehensive picture.

2. Materials and methods

The original plant taxa names used by Sillinger (1933), Krajina (1933b) and Hadač et al. (1969) are adjusted according to checklists of Marhold et al. (1998), Kubinská, Janovicová (1998) and Pišút et al. (1998); missing synonyms – mostly of mosses and lichens – were searched in online databases: The Plant List (2013), GBIF.org (2021), Plants of the World Online (2019) and Euro+Med (2006–). In special cases the original taxa names of Krajina or Hadač et al. are retained, e.g. *Senecio* ‘*nemorensis*’ which actually could represent various taxa of the genus – especially *S. hercynicus*, *S. germanicus* and their hybrid taxa in the case of Krajina’s relevés (cf. Hodálová 1999); names *Soldanella hungarica*/*S. major* are changed to *S. marmarossiensis* Klášť. in accordance with Zhang et al. (2001)⁴ [however, cf. *S. tatricola* Niederle (Niederle (2003) or *S. haretii* Grinț.⁵].

³ However, the phytocoenological methodology is further developed as well, e.g. Chytrý (2000), Chytrý et al. (2002), Tichý, Chytrý (2006), Tichý et al. (2014); though, some traditionally used popular approaches should be discontinued: Podani (2006), Kučera (2011).

⁴ See emendations by Štubňová et al. (2017).

⁵ It is not clear whether this taxon and the later described *S. marmarossiensis* Klášť. (Zhang, Kadereit [2004] vs. Niederle [2007]) really represent the same taxon, i.e., distributed also within the Western Carpathians.

Nomenclatural evaluation of the discussed syntaxa names is regulated according to the 4th edition of the phytocoenological Code (Theurillat et al. 2021), highlighted are cited Definitions (Def.), Articles (Art.) and Recommendations (Rec.).

Phytocoenological assessments and comments on the phytocoenological relevés of Krajina (1933b) and Hadač et al. (1969) discussed here are based on a syntaxonomical synthesis of natural Norway spruce woodlands of the Western Carpathians (Kučera 2012a), which was later extended by Kučera (2022, 2023).

These relevés were electronically stored using the Turboveg for Windows database software (Hennekens c1998–2020) (cf. Hennekens, Schaminée 2001) by the present author (for Kučera 2007) and submitted to the Slovak vegetation database (cf. Šibík 2012; <https://www.givd.info/ID/EU-SK-001>). The respective stored relevé data were thoroughly revised for this paper.

Subsequently they were exported to the software package JUICE (Tichý c1998–2020) (cf. Tichý 2002) for further processing. Taxa of the same species with unequal taxonomic rank were merged to the nearest mutual rank (e.g. *Solidago virgaurea* ssp. *minuta*, *Solidago virgaurea*).

The relevé data from JUICE were exported for the statistical analysis of dissimilarities performed with the software package SYN-TAX 2000 (Podani 2001a). The ordinal hierarchical clustering was carried out to correctly evaluate the quantitative information provided by the original ordinal scale of recorded data (cf. Kučera 2011), and Podani's discordance coefficient was used as it also takes into account the presence-absence relationships (Podani 2001b). Relevé ordination was performed in the same way, using non-metric multidimensional scaling (NMDS).

For the preparation of differential phytocoenological Tables 1 and 2 (see the Appendix), species records were grouped in JUICE according to the vegetation layers and, finally, with regard to their differential attributes (fidelity and frequency values); the concept of fidelity sensu Chytrý et al. (2002) was used. Only minor adjustments were applied (see chapters 3.2.1.2 and 3.2.2.2 below).

Sorting of species sequences into the vegetation layer groups in the Tables 1 and 2 follows the template of synoptic tables of the Vegetation of the Czech Republic, Vol. 4 (Chytrý et al. 2013b). Cover-abundance scores are mostly given in the originally published form – in the 11-degree Domin scale used both by Krajina (1933b; cf. 1933a, p. 778) and Hadač et al. (1969). However, certain differences in the application of some values of this cover–abundance scale occur between these two monographs (cf. Kučera msc.^A).

3. Results and discussion

3.1 Recognition of the considered syntaxa in the literature

3.1.1 *Athyrio-Piceetalia* Hadač 1962

The description of the order was one of the outcomes of the extensive field research carried out by wider group of Czech and Moravian scientists and students in the Belianske Tatry Mts (northern Slovakia). Although the research was performed between the years 1955 and 1960, the resulting monographical geobotanical surveys were published

much later by Hadač et al. (1969) and Šmarda et al. (1971).⁶ The beforehand published conspectus of vegetation units of Hadač (1962) contained the original description of the order '*Athyrio-Piceetalia* Hadač 1962' with three subordinated alliances with names as follows: (1) '*Oxalideto-Piceion* (Kraj. 1933) Břez. et Hč.' [Art. 41b], (2) '*Chrysanthemeto-Piceion* (Kraj.) Břez. et Hč.' [Art. 41b] and (3) '*Abietion* Březina et Hč in Březina 1958' [nom. nud., Art. 2b].⁷

In the former Czechoslovakia the order '*Athyrio-Piceetalia*' was immediately accepted by Holub et al. (1967) in the first release of the modern vegetation synopses, even before a comprehensive diagnosis and description of the order had been published (in 1969).⁸ Later tradition of recognition and delimitation of the order '*Athyrio-Piceetalia*' within the Czech Republic was, in all likelihood, largely influenced by the floristically and ecologically altered interpretation of this syntaxon by Sýkora (1971). Although Sýkora did not refer to the detailed survey of Hadač et al. (1969), he mentioned the order name and described a new alliance *Athyrio alpestris-Piceion* Sýkora 1971 as an independent unit apart from the existing alliances *Oxalido-Piceion* and *Chrysanthemo-Piceion*. Following the concept of Sýkora, with some remarks, the order *Athyrio-Piceetalia* was recognised within the unfinished series on the vegetation of the Czech Republic (Husová et al. 2002). On the contrary, neither the order '*Athyrio-Piceetalia*' is distinguished within the most recent vegetation survey of the Czech Republic (Chytrý et al. 2013a) – as the taxonomical rank of order was not used in the whole monograph series at all, nor its original alliances as defined by Hadač are differentiated.⁹

With a few exceptions in the 1970s, Slovakian authors consistently adopted the use of the order '*Athyrio-Piceetalia*' as characterised in detail by Hadač et al. (1969) (Fajmonová 1978, 1986, Šomšák in Mucina et al. 1985, Jarolímek et al. 2008, Kanka 2008 etc.); however, the alliance *Athyrio alpestris-Piceion* Sýkora 1971 was usually additionally included within this order (cf. Šomšák in Mucina et al. 1985, Jarolímek et al. 2008) – with the exception of the newest Slovak national survey within the monograph series *Vegetation of Slovakia* (Kliment et al. 2022; sec. Kučera 2012a, Chytrý et al. 2013a).

Within the German-speaking countries, the order '*Athyrio-Piceetalia*' was first accepted by Passarge (1978). Later it was accepted in the three-volume Austrian

⁶ Several articles and smaller monographs were, however, published earlier, e.g., Bareš, Hadač (1958), Hadač et al. (1960), Hadač, Smola (1962a), etc. (cf. Šmarda et al. 1971, p. 5).

⁷ Hadač et al. (1969, p. 289–291) also mentioned the alliance '*Athyrio-Piceion*'; however, such syntaxon was not formally recognised in that survey. Considering the presented list of mosses and vascular plants intended to contain taxa common for the alliances '*Abietion*' and '*Athyrio-Piceion*' (hence the original order name '*Athyrio-Piceetalia*'), it may be concluded that the latter name was already abandoned by Hadač before the year 1962; its use most probably reflects an anachronous version of the original manuscript and the respective paragraphs were not revised in the published version.

⁸ According to my opinion, the species list compiled by R. Neuhausl for the single differentiated subordinated alliance '*Chrysanthemo-Piceion* Krajina 1933' was, however, mostly based on works of Krajina (1933b) and Sillinger (1933; cf. *Piceetum altherbosum calcicolum*, p. 91).

⁹ Such a result is consistent with the comprehensive phytocoenological evaluation of the Western Carpathian natural *Picea abies* plant communities (e.g. Kučera 2022, 2023) because the Czech, Moravian and the adjacent S to SW Upper Silesian mountain ranges lack the adequate habitats for the development of the '*Athyrio-Piceetalia*' communities.

vegetation survey (see Wallnöfer 1993); the authors of the most recent Austrian forest vegetation survey (Willner et al. 2007) preferred the concept utilising the alliance *Abieti-Piceion* (Br.-Bl. in Br.-Bl. et al. 1939) Soó 1963 instead. The order is also included in the latest conspectus of the German vegetation (Bergmeier 2020).

The concept of a separate order '*Athyrio-Piceetalia*' was rejected in Slovenia by Zupančič (1999, repeated in 2000 and 2007), together with several misinterpretations and incorrect statements related to the survey of Hadač et al. (1969). Nevertheless, the syntaxon was accepted later (Juvan et al. 2013).

The order '*Athyrio-Piceetalia*' was first mentioned in Romania by Borhidi (1969, 1971); however, he introduced the name only as a corresponding name to his alliance '*Adenostylo-Piceion* Borhidi 1969' (nom. superfl., Art. 29c). In the current Romanian vegetation surveys the approach to the order '*Athyrio-Piceetalia*' is divided: while Chifu, Irimia (2014) accept the unit, Coldea et al. (2015) do not recognise it as a separate syntaxon at the rank of order.

The order '*Athyrio-Piceetalia*' was currently recognised also in the newest French vegetation survey by Thébaud, Bernard (2018).

The growing acceptance of the order '*Athyrio-Piceetalia*' within the system of the class *Vaccinio-Piceetea* Br.-Bl. in Br.-Bl. et al. 1939 resulted in its acknowledgement within the European vegetation conspectus of Mucina et al. (2016), although under a changed form and author citation as '*Athyrio filicis-feminae-Piceetalia* Hadač in Hadač et al. 1969' (cf. chapters 3.2.3 and 3.2.4 below); the order name was listed in the same manner in the Croatian (Željko et al. 2017), Ukrainian (Dubyna et al. 2019) and German vegetation synopses (Bergmeier 2020).

3.1.2 *Chrysanthemo-Piceion* (Krajina 1933) Březina et Hadač in Hadač 1962

This alliance was formally established by Krajina (1933b) under the name '*Chrysanthemion rotundifolii*'. Under the experience with tall forb Norway spruce phytocoenoses studied by Březina et Hadač in the Belianske Tatry Mts¹⁰ they subsequently renamed the aforementioned Krajina's alliance to '*Chrysanthemeto-Piceion*' (Hadač 1962, p. 53) to formally express the forest character of the respective communities (Hadač et al. 1969, p. 265 and 275); especially in consideration of those dominated in the field layer by *Leucanthemum* [ut *Chrysanthemum*] *rotundifolium* (Hadač et al. 1969, p. 281–283) which the authors considered to be syntaxonically identical with the physiognomically similar Krajina's '*Piceeto-Chrysanthemetum rotundifolii*' of the High Tatras (Krajina 1933b, tab. 60).

Later Slovak authors studying the similar *Picea abies* woodlands followed this concept (Fajmonová 1978, 1986, Kubiček et al. 1992, Kanka 2008, Krajčí 2008, 2009) in the terms as defined by Hadač et al. (1969) and also by Neuhausl (in Holub et al. 1967). The name was listed in both Slovakian vegetation synopses (Mucina et al. 1985, Jarolínek et al. 2008).

The alliance '*Chrysanthemo-Piceion*' was recognised in various vegetation surveys and lists outside the Western Carpathians: in Austria (Wallnöfer 1993), Slovenia (Šilc, Čarni 2012, Juvan et al. 2013), Romania (Chifu, Irimia 2014, Coldea et al. 2015), Croatia (Škvorc et al. 2017), France (Thébaud, Bernard 2018), Ukraine (Dubyna et al. 2019), Germany (Bergmeier 2020) as well as in the pan-European conspectus (Mucina et al. 2016).

¹⁰ Their own field relevés were published several years later (Hadač et al. 1969, p. 281–283).

3.1.3 *Oxalido-Piceion* (Krajina 1933) Březina et Hadač in Hadač 1962

The name of this – originally firstly positioned – alliance of the order '*Athyrio-Piceetalia* Hadač 1962' originated in a similar way to that in which the previous one did. Norway spruce plant communities documented by Krajina (1933b, tab. 61) and Hadač et al. (1969, p. 272–275), respectively, with field layer dominated by *Oxalis acetosella*, were considered to represent the same woodland community therefore the replacement name '*Oxalideto-Piceion*' was presented by Březina and Hadač to substitute Krajina's name '*Oxalidion*' (Hadač 1962; Hadač et al. 1969, p. 265).

The alliance was used in Slovakian literature less often, in the first place because the phytocoenoses corresponding to those described by Hadač et al. (1969) were only infrequently recorded in the respective high altitudes (Kanka 2008, cf. also Fajmonová 1978). Their species-poorer stands do not tend to attract scientists' attention. Decades later Hadač (1987) abandoned the use of the alliance '*Oxalido-Piceion*' as a separate unit and listed its original two associations '*Mnio spinosi-Piceetum* Hadač 1969' and '*Oxalido-Piceetum excelsae* Břez. et Hadač in Hadač et al. 1969' within the alliance '*Chrysanthemo-Piceion* (Kraj. 1933) Břez. et Hadač in Hadač 1962 sensu emend.'. Nevertheless, both Slovak vegetation synopses recognised the '*Oxalido-Piceion*' alliance (Mucina et al. 1985, Jarolímek et al. 2008).

Similarly, like Hadač (1987), and above all following the Czechoslovak synopsis of Holub et al. (1967), the authors outside Slovakia recognised only the name '*Chrysanthemo-Piceion*' for the whole group of *Picea abies* woodlands within the order '*Athyrio-Piceetalia*', including the pan-European vegetation conspectus (Mucina et al. 2016). The name '*Oxalido-Piceion*' thus remained unused outside Slovakia. The only exceptions are the studies of Passarge (1971, 1978) with various levels of debatable nomenclatural and syntaxonomical modifications.

3.1.4 *Abietion albae* Březina et Hadač in Hadač 1962

Unlike the previous two alliance names, this alliance name was published by Hadač (1962) as a nomen nudum (Art. 2b, 8). It was later validated by the author (Hadač 1965) under the name '*Abietion* Březina et Hadač 1962'/'*Abietion* Březina et Hadač in Hadač 1962' (i.e., '*Abietion albae* Březina et Hadač in Hadač 1962 ex Hadač 1965 nom. illeg.', Art. 31).¹¹ Into this alliance he grouped plant communities of *Abies alba* and *Abies alba-Picea abies* stands, typically characterised by species-rich species composition and distributed in the south-eastern part of the Belianske Tatry Mts (northern Slovakia), at their foothills and in several geographically close areas. According to Hadač's explanation, *Fagus sylvatica* was naturally absent (or very scarcely represented) in these forests due to the climatic constraints, namely the continental climate, which *Fagus* does not tolerate. Hadač (1965) mentioned the suballiance *Galio-Abietenion* Oberdorfer 1962¹² as a somewhat similar syntaxon but he emphasised the considerable

¹¹ If the shortened synoptical table of the associations published by Hadač (1965) would not be considered as a sufficient original diagnosis (Art. 7; cf. Kučera 2010b), the alliance name would have been validly described later by Hadač et al. (1969) as '*Abietion albae* Březina et Hadač ex Hadač et al. 1969'.

¹² The previous nomenclatural evaluation of the name as nomen invalidum (Kučera 2008a), cf. also Mucina et al. (2016), is no longer applicable. According to the currently revised nomenclatural rules of the Code and acceptance of "alternative names" (Def. VI, Art. 3, 22), the suballiance name *Galio-Abietenion* Oberdorfer 1962 should be regarded as validly published (Oberdorfer 1962, p. 40) because the properly referenced

representation of *Fagus* within the latter unit and its floristic difference.

Hadač's concept was accepted in later Slovak local, regional, and national vegetation surveys (Šomšák in Mucina et al. 1985, Školek 1995, Jarolímek et al. 2008, Kanka 2008). Passarge (1978) assigned the syntaxon a new name and rank, i.e. as 'Unterverband *Oxalido-Abietion* Brez. et Hadač 62 em. nom. nov.'. ¹³ This changed position of the syntaxon was accepted in some studies from Slovakia (Šomšák 1986, Kubíček et al. 1992, Šomšák et al. 1993).

Apart from the modification by Passarge (1978), the alliance '*Abietion albae* sensu Březina and Hadač' was not included in vegetation surveys of surrounding countries or elsewhere. The most notable reason was the pre-existence of ecologically and floristically more or less similar higher syntaxa (cf. overview by Kučera 2008a), i.e., suballiances *Abieti-Piceenion* Br.-Bl. in Br.-Bl. et al. 1939, *Galio-Abietenion* Oberdorfer 1962 and *Vaccinio-Abietenion* Oberdorfer 1962, even though Slovak authors distinguished Hadač's *Abietion* alliance along with Oberdorfer's suballiances (cf. Mucina et al. 1985, Jarolímek et al. 2008 and overviews of Kučera 2009c, 2010b). Therefore, the alliance '*Abietion albae*' ended up as a syntaxon with a strictly regionally recognised and limited distribution. Field research performed since the second half of the 2000s has led to a considerable reassessment of its syntaxonomical status (e.g., Kučera 2007, 2008b, 2009a, b, 2010b, 2012a, b, msc.^B).

3.2 Comparison of the relevant plant communities and nomenclatural evaluation of the corresponding syntaxa names

As the phytocoenological application of a syntaxon – i.e. in this work the discussed name of the syntaxonomical order '*Athyrio-Piceetalia* Hadač 1962' – is defined by its original diagnosis, which, in the case of higher syntaxa, is represented by their subordinated syntaxonomical unit(s), the phytocoenotic delimitation as well as the nomenclatural issues of the above-mentioned alliances '*Chrysanthemo-Piceion*' and '*Oxalido-Piceion*' have to be discussed in the first place.

3.2.1 *Chrysanthemion rotundifolii* Krajina 1933 vs. *Chrysanthemo-Piceion* sec. Hadač et al. 1969

A long time after the publication of the name '*Chrysanthemion rotundifolii* Krajina 1933', Hadač (1962) was the first who used this syntaxon name and included it in the newly described order '*Athyrio-Piceetalia* Hadač 1962'. The form of the former name was, however, modified to '*Chrysanthemeto-Piceion* (Kraj.) Břez. et Hč.' because the alliance was intended to include "Flurwälder, in denen *Picea* dominiert", i.e. [natural] tall forb Norway spruce woodland communities (see Hadač et al. 1969, p. 275–288).

It should also be reminded that Krajina (1933b, p. 145) stated that phytocoenoses which he assigned to his alliance '*Chrysanthemion rotundifolii*' were already studied

subordinated association names of '*Abietetum suevicum* Oberdorfer 1957' and '*Pyrolo-Abietetum*' had likewise been validly published by Oberdorfer (1957).

¹³ The original name '*Abietion albae* Březina et Hadač in Hadač 1962' was, however, not cited, whereas two association names that Hadač et al. (1969) had assigned to this alliance were nevertheless cited. The resulting author citation could theoretically read "*Oxalido-Abietenion* (Březina et Hadač in Hadač 1962) Passarge 1978".

by Sillinger (1933) in the Low Tatras, and that the latter author described a plant community under the association name '*Piceetum altherbosum silicicolum* (Sillinger 1933) Krajina 1933' [nom. illeg. (Art. 34a) $\equiv$ subass. '*Piceetum altherbosum silicicolum* Sillinger 1933' nom. illeg., Art. 13a, 34a].

From the nomenclatural point of view, Kučera (2010a, 2012a) assessed the name '*Chrysanthemeto-Piceion* (Kraj.) Brez. et Hč.' as invalidly published by Hadač (1962) and therefore proposed to use only the name '*Oxalido-Piceion* Hadač et al. 1969' (cf. chapter 3.2.2.4 below). Moreover, he discussed several aspects of the original and later application of the alliance name '*Chrysanthemo-Piceion*' (Kučera 2007, 2010c/2012a). The proposal to disregard the validity of the '*Chrysanthemo-Piceion*' name published by Hadač (1962) was, however, not justified (see chapter 3.2.1.3 below).

Anyway, the continuing traditional use of the name '*Chrysanthemo-Piceion* (Krajina 1933) Brezina et Hadač in Hadač 1962' to the present (cf. Mucina et al. 2016, Kliment et al. 2022) is the reason why the adequacy of the syntaxonomical application of this alliance name needs to be questioned (see below).

3.2.1.1 Norway spruce-*Leucanthemum rotundifolium* plant community of Krajina (1933b)

The two-part monograph of Krajina (1933a, b) focused on the vegetation of the Mlynická dolina Valley in the High Tatras where various alpine vegetation types naturally prevail due to high altitudes of this territory. Only in its lowermost part are scrub and forest communities developed.¹⁴ Krajina (1933b, p. 145) differentiated five associations – and altogether eight syntaxa – which he placed within the order '*Piceetalia abietis*': two associations and two subassociations of them are commonly considered as forest communities.

The first introduced association was '*Piceeto-Chrysanthemetum rotundifolii* (*Picea abies*-*Chrysanthemum rotundifolium*-Assoziation.)' (Krajina 1933b, p. 145 ff.). The author described it as a highly characteristic but spatially restricted plant community occurring in the transitional zone between Norway spruce forest and dwarf mountain pine krummholz. He documented it with six phytocoenological relevés recorded mostly on the stream banks of the Mlynica Brook in the altitudinal range 1,430–1,545 m a. s. l. (Krajina 1933b, Tab. 60, p. 148–151 + p. 147).

My informative field examination at the locus classicus of this association – i.e. the glacially-formed Mlynická dolina Valley (the High Tatras) and its opening – confirmed that the respective plant community with the field layer consisting of *Leucanthemum rotundifolium*, *Senecio subalpinus*, *Aconitum firmum*, *Chaerophyllum hirsutum*, *Phyteuma spicatum* etc. is still present in the territory (9. 9. 2009, P. Kučera, photo). Exactly as Krajina (1933b, p. 145–147) indicated, these phytocoenoses are usually forming small stands and they inhabit mostly the left and right banks of the Mlynica Brook.

However, it should be specified in more detail that the considered plant community is developed there directly on the Mlynica stream: its stands only infrequently extend more than 2–3 metres from the stream itself (see Figs. 1, 2). The other occurrences of the association stands which are not associated with the Mlynica's stream dwell on

¹⁴ The largest part of the considered forested area, i.e. the elevations approximately below the 1,450 m contour line belongs, however, geomorphologically not to the region of the High Tatras but to a special subunit of the Podtatranská Kotlina Basin labelled as "Tatranské podhorie" [Tatra foothills] (see Kočícký, Ivanič 2011).



Fig. 1. Typical streamside habitat of a *Leucanthemum rotundifolium* plant community within the woodlands surrounding the Mlynica stream in the High Tatras (Kučera 2012a, p. 338, fig. 16: P. Kučera, 9. 9. 2009)



Fig. 2. Another example of a typical *Leucanthemum rotundifolium* community habitat below the Mlynická dolina Valley in the High Tatras (P. Kučera, 9. 9. 2009).

habitats bound to ecologically similar places with a high water supply as Krajina (1933b, p. 146) already stressed: small streams, small swampy terrain depressions, or spring areas. Due to glacially formed relief, those habitats are often full of boulders, or the water stream is present close the bouldery surface. Habitat slope inclination is considerably small (0–15 °), soil is not very deep (10–60 cm) and considerably acidic (Krajina 1933b, p. 146, 151) because the glacially formed landscape of the studied area originated from granitic rocks of the High Tatras – granodiorites to tonalites (Nemčok et al. 1993).

The historically declared and recently confirmed riparian and other specified occurrences of Krajina's Norway spruce-*Leucanthemum* plant community correspond also with the recorded cover values of *Picea abies* (*Pinus cembra*) or *Pinus mugo* in Krajina's relevés (1933b, tab. 60). Cover of *Picea abies* trees within his relevés reached at most Domin cover-abundance scores 3 and 4 (cf. Krajina 1933a, p. 778; i.e. 5 to up approximately 15 % of the relevé plots [cf. Hadač et al. 1969, p. 17]), with one exception of score 6 in the relevé No. 4 (i.e. between 25–33 %; see Appendix: Tab. 1, rel. 4). Similar cover values were visually confirmed in situ during recent field examination; however, the corresponding plant community is frequently developed also completely without any cover of *Picea abies* trees (see Figs. 1, 2).

Attention should be called to the sizes of Krajina's original relevé plots. The values range between 6–80 (300) m². Such sizes are unusual for a supposed forest community – they may reflect the real size limits of the respective continuous areas of the community stands (cf. Krajina 1933b, p. 145). Such conclusion is in accordance with my recent field examination. Noticeable is also the striking contrast between the stated total canopy cover values and the recorded tree and shrub species cover-abundances (see Appendix: Tab. 1); the conducted field investigation supports the view that only the latter values should be the more accurate ones within Krajina's records of Norway spruce-*Leucanthemum* community.

Since the year 2009, I have noticed phytocoenoses corresponding to '*Piceo-Chrysanthemetum rotundifolii* Krajina 1933' also in other localities of the High Tatras (e.g. the Mengusovská dolina Valley). In the same way as described above, their habitats are found on the brook banks, along the small streams and streamlets or directly within them in the depressions and so on. The *Picea abies* trees usually only overshadow parts of the *Leucanthemum*-stands from their borders or from further away as they usually grow outside of such water-enriched habitats. Sometimes, *Picea* or *Pinus mugo* individuals are growing within the respective *Leucanthemum*-stands; however, they are rooted on larger boulders and thus in a different habitat type than the one of '*Piceo-Chrysanthemetum rotundifolii*'.

In accordance with my field knowledge, it is here concluded that the original diagnosis of the association '*Piceo-Chrysanthemetum rotundifolii* Krajina 1933' represents a non-forest plant community of riparian and similar water-influenced habitats of the supramontane–alтимontane (? subalpine) zones and that it should not be included among woodland plant communities. This is ultimately the reason why Krajina (1933b, p. 145, 147) himself already admitted the alternative classification of the alliance *Chrysanthemion rotundifolii* Krajina 1933 within the order *Adenostyletalia* Br.-Bl. 1930. Within the locus classicus, stands of *Piceo-Chrysanthemetum rotundifolii* Krajina 1933 are sometimes associated with *Aconitum firmum*- or *Adenostyles alliariae*-communities of the class *Mulgedio-Aconitetea* Hadač et Klika in Klika 1944.

3.2.1.2 *Leucanthemum rotundifolium*-Norway spruce plant community of Hadač et al. (1969)

A wide collective of scientists and students under the leadership of Hadač carried out comprehensive field research in the Dolina Siedmich prameňov Valley¹⁵ situated in the south-eastern part of the Belianske Tatry Mts (small easternmost section of the Tatra Mountains). The complex study of all plant communities in the delimited area also included woodlands which were, however, considerably reduced in their spatial extent at that time (cf. Hadač, Smola 1962a, and photos in Hadač et al. 1960, 1969, Šmarda et al. 1966, 1971, *Historická ortofotomapa Slovenska* [s. d.]). Norway spruce stands constituted the prevailing portion of the then forested area.

The phytocoenological study by Hadač and coll. revealed, among others, three types of species-rich tall forb/tall fern Norway spruce woodlands, one of which was dominated by *Leucanthemum rotundifolium* and *Athyrium filix femina*, *Dryopteris filix-mas*, (*Senecio 'nemorensis'*), in the field layer. According to Hadač et al. (1969, p. 281–283), *Picea abies* dominates in the tree layer, and *Sorbus aucuparia* and *Larix decidua* ssp. *polonica* are usually admixed.

The authors came to the conclusion that this specific Norway spruce community is syntaxonically identical with '*Piceo-Chrysanthemetum rotundifolii* Krajina 1933' (cf. Hadač et al. 1969, p. 275, 280) and they proposed the inversion of this name to the form '*Chrysanthemo-rotundifolii-Piceetum* Krajina 1933' in order to formally express the forest character of the studied plant community.

Habitat properties of the four samples of *Leucanthemum rotundifolium*-Norway spruce phytocoenoses documented by Hadač et al. (1969) are quite distinct in comparison with ecological conditions described by Krajina (1933b, p. 146 ff.; see above): altitude elevations of the recorded relevés are considerably lower – 1,250–1,325 m (overall distribution of the community is given as 1,200–1,400 m a. s. l.), the slopes are steep (30–40 °), the geological background is formed by limestones, the soils are around 1 m deep rendzinas. It is definitely not a water-logged habitat as in the case of Krajina's (1933b) Norway spruce-*Leucanthemum* community. Physiognomically the most striking difference is the fact that Hadač et al. (1969) recorded a real forest community with a dominance of *Picea abies* in the tree layer reaching Domin cover-abundance scores 7 and 8 (i.e. up to 50 or 75 % of the total sample areas). Problematic are, however, unusual sizes of the respective relevés: 100, 100, 35 and 45 m². This fact is probably the reason why Šmarda et al. (1971) did not record – within the same studied area – such *Leucanthemum rotundifolium*-Norway spruce community as a separate syntaxon and why they classified somewhat similar relevés within the facies '*Sorbeto-Piceetum calcicolum altherbosum*' (cf. also Šmarda 1966a, b).

The considerably different habitat is the unequivocal reason why the *Leucanthemum*-woodland recorded by Hadač et al. (1969) is fundamentally very different from the Norway spruce-*Leucanthemum* relevés published by Krajina (1933b) (see Appendix: Tab. 1) which is evident especially from the long list of differential species between the compared plant communities. In contrast to the above-discussed Krajina's riverine acidic *Leucanthemum* plant community of the High Tatras, the cited community

¹⁵ It should be reminded that this valley name was at that time applied to a different, spatially much narrower area than in later decades (Kučera 2009; see Hadač et al. 1960, p. 15).

from the Belianske Tatry Mts represents one of the types of mesic calcicolous forest communities of the higher montane altitudes in the higher Western Carpathian mountain ranges.

This forest plant community labelled by Hadač et al. (1969) [and their followers, cf. chapter 3.1.2 above] as '*Chrysanthemo-rotundifolii-Piceetum* Krajina 1933' and similar *Picea*-dominated phytocoenoses of montane altitudes are, however, not stable communities. The recently recorded spread of *Acer pseudoplatanus*, *A. platanoides* and *Fagus sylvatica* within the slopes of the Dolina Siedmich prameňov Valley [in the current spatial delimitation] has the form of a spontaneous reverse succession, expanding to the places of their original natural distribution. *Abies alba* was also a regular component of the original woodlands. During the field research of the territory, I have confirmed the presence of older *Fagus* and *Abies* trees as well (Kučera 2009c); sporadic occurrence of silver fir in higher elevations referred by Hadač et al. (1960) [cf. Hadač 1987] should be also explained by (proto)historic anthropogenic land management.

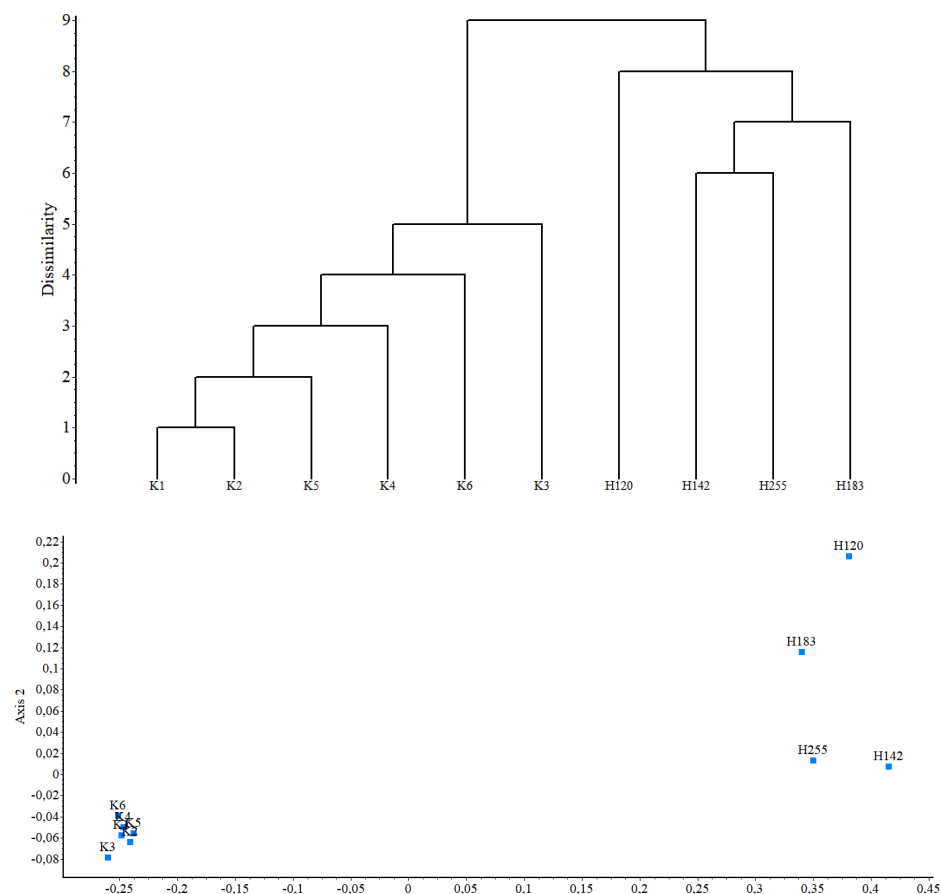
The recorded territory-wide dominance of *Picea abies* is therefore the result of centuries long anthropogenic influence on the forests of this region. The same origin has also the presence of *Larix* as light-demanding species in the habitats of the recorded relevés of '*Chrysanthemo rotundifolii-Piceetum*' within the territory of the Dolina Siedmich prameňov Valley as well as in the whole Belianske Tatry Mts (cf. Hoľub-Pacewiczowa 1931, Plesník 1971, Bohuš 1972, 1994a, b; see also Bareš, Hadač 1958, Hadač, Smola 1962a, Hadač et al. 1969, p. 14–16, Šmarda et al. 1971, Kučera 2012a, chapter 5.15). Moreover, the extent of deforestation of the Tatra Mountains during the existence of the protohistorical Púchov culture (Iron Age and part of Roman period) is not reliably known (cf. Plesník 1971, Pieta 2010). Impact of ancient cultures on the tree species composition of forests in the sub-Tatric region, especially on the presence of *Fagus*, however, is clearly documented (Krippel 1963; cf. discussion by Kučera 2015).

(Proto)historically) changed tree species composition in favour of conifers (*Picea abies*, *Abies alba*) manifested by the corresponding change in species presence and/or cover-abundances (see chapter 3.2.2.1 below) is more pronounced in lower elevations equivalent to the altitudinal occurrence of *Leucanthemum rotundifolium*-Norway spruce community recorded by Hadač et al. (1969) and below. Under such anthropogenically induced conditions some grasses and herbs profit from absence of litter fall from deciduous trees (especially *Fagus*) therefore their expansion is enabled. On calcicolous bedrock such "*Picea/Abies*-positive species" are, e.g., *Carex alba*, *Calamagrostis arundinacea*, *Poa stiriaca*, *Fragaria vesca*, *Leucanthemum rotundifolium*, *Melampyrum sylvaticum*, *Moneses uniflora*, *Oxalis acetosella*, *Orthilia secunda*, *Rubus saxatilis*, etc. (cf. Šmarda 1966a, Hadač et al. 1969, Šomšák 1986).

As such, this *Leucanthemum*-rich Norway spruce woodland of the Belianske Tatry Mts might represent a temporal forest stage developed under the ecological influence of increased light availability under the crowns of *Sorbus aucuparia* and *Larix decidua* ssp. *polonica* and, at the same time, a reduced *Picea* cover. These phytocoenoses syntaxonically do not belong to the class *Vaccinio-Piceetea* Br.-Bl. in Br.-Bl. et al. 1939: they represent a substitute subanthropogenic mixed *Picea* forest form of montane mixed *Fagus-Abies-Picea* forests of the class *Carpino-Fagetea* Jakucs ex Passarge 1968 (Kučera 2012a).

Although Hadač et al. (1969) claimed that they documented vegetation samples of the same plant association as Krajina (1933b) [i.e. '*Piceo-Chrysanthemetum rotundifolii* Krajina 1933'], the recent direct comparison of relevés recorded by Krajina and Hadač et al., respectively, displayed considerable floristical differences (Kučera 2012a, p. 196–197). Statistical dissimilarities among the relevés examined are depicted by their clustering pattern in the dendrogram (Fig. 3) and by their positions within the ordination diagram (Fig. 4).

The here presented differential phytocoenological Table 1 (see Appendix) is a revised version of the aforementioned comparison. Less frequently occurring species in the respective community and selected species occurring in both communities are also included among the differential species because their presence and/or recorded cover-abundance scores are ecologically specific to plant communities of either Krajina or Hadač et al. Chosen characteristics of relevé plots are also attached for a better comparison.



Figures 3 and 4. Grouping of the respective *Leucanthemum*-rich relevés of Krajina (1933b: “K”) and Hadač et al. (1969: “H”) according to hierarchical clustering (dendrogram) and ordination (scatter plot). For numbering see Tab. 1 in the Appendix.

Differential species of Krajina's community '*Piceo-Chrysanthemetum rotundifolii* Krajina 1933' against '*Chrysanthemo-Piceetum* sec. Hadač et al. 1969' (Appendix: Tab. 1) – *Viola biflora*, *Aconitum firmum*, *Alchemilla* spp., *Potentilla aurea*, *Senecio subalpinus*, *Chaerophyllum hirsutum*, etc. are bound to the wet habitat of the former *Leucanthemum*-community which, as shown above, does by no means belong to true Norway spruce woodlands. The mentioned species group rarely (if at all) enter the surrounding silicicolous *Picea* woodlands, as they require a sunny and at the same time flowing-water supplied habitat.

Moreover, the detailed survey of all available phytocoenological relevés and additional geobotanical data on Slovakian/Western Carpathian *Picea abies* woodlands which I performed for my doctoral thesis (Kučera 2010c, publ. 2012a) revealed that, besides Krajina (1933b) himself, no other author ever published or recorded a Norway spruce-*Leucanthemum* phytocoenosis corresponding to '*Piceo-Chrysanthemetum rotundifolii* Krajina 1933' in the Western Carpathians (cf. also Šmarda et al. 1971, Matuszkiewicz 2002, Kliment et al. 2022, Kučera 2023, msc.^B).

3.2.1.3 Nomenclatural and syntaxonomical consequences with summary

(I) A detailed comparison of the original characteristics of the phytocoenoses of Krajina vs. Hadač and coll. indicates that the respective authors documented not only two considerably distinct plant communities of different vegetation formations but, above all, two completely different habitats.

The above explained differences indicate that the proposals (1) to invert the association name '*Piceo-Chrysanthemetum rotundifolii* Krajina 1933' to the form '*Chrysanthemo rotundifolii-Piceetum* Krajina 1933' published by Hadač et al. (1969) as well as (2) to change its superordinated alliance name '*Chrysanthemion rotundifolii* Krajina 1933' to the form '*Chrysanthemo-Piceion* (Krajina 1933) Březina et Hadač in Hadač 1962' published beforehand by Hadač (1962) have arisen from a misidentification of the plant communities documented by Krajina (1933b) and Hadač et al. (1969), respectively. In spite of this erroneous outcome, the syntaxonomical concept proposed by Hadač (1962) and specified in detail by Hadač et al. (1969) was fully followed by later authors up to the present (cf. Mucina et al. 2016, Kliment et al. 2022).

(II) As a collateral result, the original name '*Chrysanthemion rotundifolii* Krajina 1933' is given as an example of an illegitimate name within the recent edition of the syntaxonomical Code (Theurillat et al. 2021, p. 31: Art. 29b) although such evaluation does not fully correspond to its factual original diagnosis.

A hypothetical solution would be the exclusion of the association '*Piceo-Chrysanthemetum rotundifolii* Krajina 1933' from the alliance '*Chrysanthemo-Piceion* (Krajina 1933) Březina et Hadač in Hadač 1962' and at the same time the retaining of the latter unit as a valid syntaxon on the basis of Krajina's (1933, p. 145) evaluation that the association '*Piceetum altherbosum silicicolum* (Sillinger 1933) Krajina 1933' also belongs to the alliance '*Chrysanthemion rotundifolii* Krajina 1933'.

However, even if the respective original relevés of Sillinger's (1933) plant communities 'Type *Adenostyles alliariae*' and 'Type *Athyrium alpestre*' originally described within the subassociation '*Piceetum altherbosum silicicolum* Sillinger 1933' would represent natural Norway spruce woodlands (which they do not, see Kučera 2023!), then:

- the former plant subcommunity would have a very problematic position within

the frame of the traditional application of the name '*Chrysanthemo-Piceion*', at least in Slovakia, which corresponds to the designation '*Chrysanthemo rotundifolii-Piceion* sec. Hadač et al. 1969' [i.e. '*Chrysanthemo rotundifolii-Piceion* auct. non Krajina 1933']; there it could represent at most a kind of silicicolous opposite to the association '*Adenostylo alliariae-Piceetum abietis* Samek et al. 1957 nom. corr. et nom. cons. propos.' (cf. Kučera 2022, msc.^{B)};

– the latter plant subcommunity, dominated in the field layer by *Athyrium distentifolium*, should be classified syntaxonomically within the traditionally used alliance *Athyrio alpestris-Piceion* Sýkora 1971 [and therefore within the alliance *Piceion abietis* Pawłowski ex Pawłowski et al. 1928 nom. corr. (Art. 44): Exner 2007, Kučera 2010a, 2010c/2012a, Chytrý et al. 2013].

Such an approach has been, however, hardly ever applied (cf. Kučera 2022 and 2023, Kliment et al. 2022¹⁶). Special case is the proposal of Mucina et al. (2016) to synonymise '*Chrysanthemo rotundifolii-Piceion* (Krajina 1933) Březina et Hadač in Hadač 1962' and '*Athyrio alpestris-Piceion excelsae* Sýkora 1971'. The original diagnosis of the alliance '*Athyrio alpestris-Piceion* Sýkora 1971' as defined by its original author (Sýkora 1971, p. 43–44, 47–49), however, definitely does not correspond to the vegetation type labelled as "Mesic herb-rich spruce forests of the Central and Northern European mountains" as given by Mucina et al. (2016, p. 32).

Syntaxonomical use of the alliance name '*Chrysanthemo-Piceion*' by Hadač et al. (1969) and all the other authors (see chapter 3.1.2. above) correspond to that of a pseudonym (cf. Def. X) – '***Chrysanthemo-Piceion* auct. non Krajina (1933) Březina et Hadač in Hadač 1962**', or, more specifically, '*Chrysanthemo-Piceion* sensu Hadač et al. 1969 non (Krajina 1933) Březina et Hadač in Hadač 1962'. The factual syntaxonomical use of the pseudonym '*Chrysanthemo-Piceion* auct. non Krajina (1933) Březina et Hadač in Hadač 1962' in the European literature is the source of ongoing various multiple confusing and incorrect statements and evaluations.

(III) The presented case of the substantial floristical and ecological difference between the *Leucanthemum*-communities of Krajina (1933b) vs. Hadač et al. (1969), respectively, has four nomenclatural and syntaxonomical consequences:

A) The original diagnosis of the association commonly cited as '*Chrysanthemo rotundifolii-Piceetum* Krajina 1933' (i.e. as nomen inversum [Art. 42] compared to its original form published by Krajina [1933b]) represents a non-forest plant community syntaxonomically belonging to the class *Mulgedio-Aconitetea* Hadač et Klika in Klika 1944. The original form of the name, i.e. '*Piceo-Chrysanthemetum rotundifolii* Krajina 1933' should be therefore maintained. The lectotypification of this association by Kučera (2010a) – although performed under the inversed name '*Chrysanthemo rotundifolii-Piceetum*' – remains valid.

B) In the same manner, the respective alliance name should be used in the form '*Chrysanthemion rotundifolii* Krajina 1933' whereas the "corrected" form – in the terms of Hadač et al. (1969, p. 265, 275), i.e. '*Chrysanthemo-Piceion* (Krajina 1933)

¹⁶ A peculiar approach is adopted in the latter revision of the '*Vaccinio-Piceetea*' communities in Slovakia: the association '*Piceo-Chrysanthemetum rotundifolii* Krajina 1933' is there characterised as the only original element of the alliance '*Chrysanthemion rotundifolii* Krajina 1933'; however, the former unit was not recognized within the renamed alliance '*Chrysanthemo-Piceion* (Krajina 1933) Březina et Hadač in Hadač 1962' which the authors regarded as a syntaxon of forest communities, nor was any explanation for such exclusion given.

Březina et Hadač in Hadač 1962', should be rejected as nomen superfluum (cf. Art. 29c) as well as an inappropriate name (cf. Art. 10). This alliance should be integrated in the syntaxonomical system of the class *Mulgedio-Aconitetea* Hadač et Klika in Klika 1944 – and following the statement of Krajina (1933b, p. 145, 147) into the order *Adenostyletalia alliariae* Br.-Bl. 1930.

C) The original content of the syntaxon corresponding to the name '*Chrysanthemo rotundifolii-Piceetum* sec. Hadač et al. 1969' – i.e. to the pseudonym '*Chrysanthemo rotundifolii-Piceetum* sensu [Krajina 1933] Hadač et al. 1969 non Krajina 1933' – represents a mixed anthropogenic calcicolous *Picea abies* woodland of the class *Carpino-Fagetea* Jakucs ex Passarge 1968. The classification of this plant community within the class *Vaccinio-Piceetea* Br.-Bl. in Br.-Bl. et al. 1939 is therefore inadequate.

D) The same applies to the alliance pseudonym '*Chrysanthemo-Piceion* sensu Hadač et al. 1969 non (Krajina 1933) Březina et Hadač in Hadač 1962'. The most of the other relevés recorded by Hadač et al. (1969, p. 275–288) represent similarly anthropogenic *Picea abies* woodlands with a natural spontaneous reverse succession of *Fagus sylvatica* (Kučera 2009a, 2012a). They syntaxonomically belong to the class *Carpino-Fagetea* Jakucs ex Passarge 1968, within the group of mesic calcareous woodlands. Only the relevés classified within the association *Adenostylo alliariae-Piceetum* Březina et Hadač in Hadač et al. 1969 nom. illeg. (Art. 31) (Hadač et al. 1969, p. 284 ff.) partly belong to the natural Norway spruce woodlands, i.e. to the class *Vaccinio-Piceetea* Br.-Bl. in Br.-Bl. et al. 1939.

The resulting conclusion is that there is no reasonable use for a syntaxon corresponding to the pseudonym '*Chrysanthemo-Piceion* sensu Hadač et al. 1969 non (Krajina 1933) Březina et Hadač in Hadač 1962' within the class *Vaccinio-Piceetea* Br.-Bl. in Br.-Bl. et al. 1939 s. str.¹⁷ representing natural *Picea abies* communities of Europe.

For consolidation of the syntaxonomical application of the alliance name '*Chrysanthemion rotundifolii* Krajina 1933', the following typification is given considering the general phytocoenological treatment of the alliance by its author (Krajina 1933b, p. 145–152):

Chrysanthemion rotundifolii Krajina 1933 (Krajina [1933b], p. 145)

Nomenclatural type: *Piceo-Chrysanthemetum rotundifolii* Krajina 1933, Krajina (1933b, p. 146, ut '*Piceeto-Chrysanthemetum rotundifolii*'), lectotypus hoc loco.

3.2.2 *Oxalidion acetosellae* Krajina 1933 vs. *Oxalido-Piceion* sensu Hadač et al. 1969

Analogous to the case of the alliance name '*Chrysanthemion rotundifolii* Krajina 1933' (see chapter 3.2.1 above), Hadač (1962; see Hadač, Smola 1962b as well) published a changed version of the original Krajina's name '*Oxalidion acetosellae* Krajina 1933' to the form '*Oxalideto-Piceion* (Kraj. 1933) Břez. et Hč.'. Reason of this approach was later explained by Hadač et al. (1969, p. 265): Krajina's nomenclature of the respective plant communities was considered misleading as a syntaxon name should indicate that it represents a Norway spruce forest community, especially in the case when *Picea abies* is the exclusive edificator of [natural] low forb Norway spruce woodland communities classified within that alliance.

Kučera (2007, 2010a) assessed the name '*Oxalido-Piceion* (Krajina 1933) Březina

¹⁷ I.e. excl. class *Piceo obovatae-Abietetea sibiricae* P. Kučera 2023.

et Hadač in Hadač 1962' as invalidly published, and he suggested that the name '*Oxalido-Piceion* Hadač et al. 1969' should instead be regarded as validly published. In consideration of the substantially homogeneous floristic composition of the Western Carpathian calcicolous *Picea abies* woodlands and the phytocoenologically different delimitation of the above-mentioned alliance '*Chrysanthemo-Piceion*' – unsuitable for the respective group of woodland plant communities, he proposed that the name '*Oxalido-Piceion* Hadač et al. 1969' should be adopted. However, this proposal to disregard the validity of the name published by Hadač (1962) was incorrect (see chapter 3.2.2.4).

In the survey of Mucina et al. (2016), the name '*Oxalido-Piceion excelsae* (Krajina 1933) Březina et Hadač in Hadač 1962' was evaluated as a synonym of the name '*Piceion excelsae* Pawłowski ex Pawłowski et al. 1928' although such an interpretation is in serious conflict with the ecological and floristic delimitation of the former alliance as defined in detail by Hadač et al. (1969) and followed by later authors (chapter 3.1.3 above).

Because the alliance '*Oxalido-Piceion* (Krajina 1933) Březina et Hadač in Hadač 1962' was chosen by Jirásek (2002) as the lectotype of the name '*Athyrio-Piceetalia* 1962', very important nomenclatural and syntaxonomical consequences connected with a re-evaluation of the nomenclatural proposal of Kučera (2010a) concerning the alliance name '*Oxalido-Piceion*' and subsequently regarding the name '*Athyrio-Piceetalia*' have to be discussed in more detail (see chapters 3.2.2.3 to 3.2.3 below). Following the aforementioned syntaxonomical proposal of Mucina et al. (2016), the order *Athyrio-Piceetalia* Hadač 1962 had to be therefore evaluated as a later synonym of the order *Piceetalia abietis* Pawłowski ex Pawłowski et al. 1928 (sic!).

3.2.2.1 *Oxalis*-Norway spruce plant community of Krajina (1933b)

The association '*Piceetum abietis oxalidetosum acetosellae silicicolum*' is the second plant community introduced by Krajina (1933, p. 153 ff.) within the order *Piceetalia abietis* Pawłowski ex Pawłowski et al. 1928. By this name he labelled distinctive, mostly low-forb Norway spruce forest plant community differentiated into two different facies: '*typicum*' and '*homogynosum*' documented by altogether 11 phytocoenological relevés (6 and 5, respectively) from elevations 1,355–1,500 and 1,300–1,475 m a s. l., respectively (Krajina 1933b, Tab. 61, p. 156–159 + p. 154–155). However, Krajina stated that the altitudinal distribution of this association extends altitudinally far down beyond the studied territory. In contrast to the original diagnosis of the above-discussed association '*Piceo-Chrysanthemetum rotundifolii* Krajina 1933', only some of the relevé sites of his relevés of the both facies of '*Piceetum abietis oxalidetosum acetosellae silicicolum*' were located at "left or right banks of the Mlynica Brook".

The *Oxalis*- or (*Calamagrostis*)-*Homogyne*-dominated field layer patches of the respective *Picea abies* woodland appeared in spatially limited areas because of the prevalence of either *Vaccinium myrtillus*- or *Calamagrostis villosa*-Norway spruce woodlands (Krajina 1933b, p. 155). Very high cover of *Picea abies* trees was particularly important for the development of the Krajina's *Oxalis*-Norway spruce community. Recorded slope inclination was small to moderate (5–25 °, microlocally to 35 °), and the soil was strongly to extremely acidic (Krajina 1933b, p. 155–159) because it developed on the granitic rocks of till forming the ground moraine during



Fig. 5. Typical Norway spruce woodland on bottom of the valley below the Mlynická dolina opening, further away from the Mlynica stream (P. Kučera, 9. 9. 2009).



Fig. 6. Another example of Norway spruce woodland in the studied region below the Mlynická dolina, with patches of *Oxalis acetosella* and *Homogyne alpina*, respectively (P. Kučera, 9. 9. 2009).

the Last Glacial (cf. Figs 3, 4). Acidic character of habitats is manifested by occurrence of common species of the order *Piceetalia abietis* Pawłowski ex Pawłowski et al. 1928 nom. corr., such as *Avenella flexuosa*, *Calamagrostis villosa*, *Vaccinium vitis-idaea*.

My field examination (9. 9. 2009) in the region of the locus classicus of '*Piceetum abietis oxalidetosum acetosellae silicicolum*' confirmed the presence of both *Oxalis*- and *Homogyne*-dominated phytocoenoses within the *Picea abies* woodlands of the area studied by Krajina (1933b); the corresponding communities are currently syntaxonomically classified within the association *Lophozio-Piceetum* Volk in Br.-Bl. et al. 1939 (Kučera 2023).

However, unlike the above-commented Krajina's Norway spruce-*Leucanthemum* community, the respective *Oxalis*-Norway spruce phytocoenoses and habitats are usually not situated directly on the Mlynica Brook banks. Krajina's (1933, p. 154) localisation of the relevé sites thus indicates a rather generalised location of these sites within the studied area considering the stream of Mlynica.

Due to prevailing bouldery character of the relief at the area studied by Krajina, *Oxalis*- and *Homogyne*-dominated *Picea* stands are mostly substantially limited in their spatial extent. They prefer habitats with deeper soil, developed between boulders or here and there on well-drained flat places. Such sites were, however, generally influenced by historical land management, especially by high-mountain pasture. Last remnants of former *Nardus stricta* stands typically accompanied by *Carex ovalis*, *C. canescens* are still present in the mentioned area as well as in other High Tatras' valleys (P. Kučera, 2009–2020, not.). Floristic composition of some Krajina's relevés is affected by historical deforestation and pasture as well as indicated by the apophytic occurrences of some species (e.g., *Ligusticum mutellina*, *Oreogalum montanum*, *Potentilla aurea*).

The tree species composition of the respective forest stands was altered in the past as well, within the whole elevation range of Krajina's relevés, and even more strongly around the contemporary upper forest line markedly affected by centuries long historical deforestation (absence of naturally developed altimontane zone of mixed *Pinus cembra* stands in the valley bottom); within the conducted field examination, I confirmed the presence of *Abies alba* growing in the area as a lower tree even at the altitude 1,529 m a. s. l. (Kučera 2012a as "1,522 m"). This is especially true also for the territory below the Mlynická dolina Valley itself where Krajina (1933b) mentioned the continuation of altitudinal distribution of the '*Piceetum abietis oxalidetosum acetosellae silicicolum*' stands (see below, cf. Kučera 2012a, msc.^B).

Generally, silver fir was primarily more frequently represented in the elevations above 1,400 m a. s. l. The presupposed occurrence of natural non-mixed *Picea abies* forests below this altitudinal limit is questionable according to my current knowledge of this region. Furthermore, forest stands with sites of Krajina's relevés situated below the elevation ca 1,360–1,370 m a. s. l. (mostly relevés of the *Homogyne* facies) should be regarded in particular as anthropogenically degraded forests. Species composition of their field layer and soil conditions would be under natural conditions of unmanaged forest influenced by presence of *Abies alba* along with *Acer pseudoplatanus* – the crucial ecological influence being litterfall of these species (and insolation regime in the case of the latter one) in comparison to non-mixed *Picea* stands. Towards the lower altitudes *Fagus sylvatica* also primarily co-influenced the habitats (Krippel 1963, 1986; cf. Kučera 2012a, 2015). All these forest stands represent substitute (sub)anthropogenic woodlands

developed on sites of original communities of the class *Carpino-Fagetea* Jakucs ex Passarge 1968; they should be syntaxonomically classified accordingly within that class, mostly in the order *Luzulo-Fagetalia* Scamoni et Passarge 1959 (Kučera 2023).

Centuries-long transformation of the original mixed forests (with or without *Picea* as their natural component) into uniformly coniferous *Picea abies* stands, here and there also with episodes of deforestation and pasture (cf. Hoľub-Pacewiczowa 1931, Krajina 1933a, p. 784, Häufler 1955, Podolák 1967, Novák et al. 2013;¹⁸ cf. also Svoboda 1936, 1940, Plesník 1971, Pieta 2010), has collateral influence on the field and ground layer species composition; a similar impact results from artificially only increased proportion of *Picea abies* in managed forest stands (Máliš et al. 2012, Verstraeten et al. 2013, Martinák et al. 2014, Kutnar 2023, etc.). Similar ecological influence has secondary, sub-/anthropogenic expansion and/or dominance of *Abies alba* (cf. Ellenberg 1963, p. 260).

Picea abies as a dominant, however, anthropogenic habitat edificator (and similarly *Abies alba* of subanthropogenic origin) has distinct impact on ecological regime of phytocoenoses, particularly on terricolous moss species enrichment and their cover expansion of ground layer of forest phytocoenoses.¹⁹ And conversely, such “*Picea*-positive” (or, more generally, “conifer-positive”) moss species are subsequently considered to be reliable indicators of the naturalness of respective mixed coniferous/*Picea abies* stands (cf. Braun-Blanquet et al. 1939, p. 13 ff., Kuoch 1954, Meyer 1954, Ellenberg 1963, p. 257 ff./1996, p. 321 ff.). It should be therefore emphasised that cover-abundances and species composition of mosses within the Krajina’s (1933b) relevés of ‘*Piceetum abietis oxalidetosum acetosellae silicicolum*’ were likewise affected by historical land management in the same manner; moreover, it should be noted that his taxa determinations may be unreliable (Hadač 1956, cf. Váňa 1997).

Interesting aspect of the original description of the association ‘*Piceetum abietis oxalidetosum acetosellae silicicolum* Krajina 1933’ [nom. inval., Art. 3e] is the name ‘*Piceetum excelsae normale silicicolum* Sillinger 1933’ given by Krajina (1933b, p. 154) as a [heterotypic] synonym. For more detailed commentary on the latter name see below chapter 3.2.2.4, section #3.

3.2.2.2 *Oxalis*-Norway spruce plant community of Hadač et al. (1969)

Hadač et al. (1969, p. 265 ff.) described two separate Norway spruce communities within the ‘*Oxalido-Piceion*’ alliance in their complex vegetation survey of the Dolina Siedmich prameňov Valley in the Belianske Tatry Mts. The first is a *Mnium spinosum*-dominated woodland with densely closed *Picea abies* canopy and poorly developed moss- and herbaceous layer (‘*Piceetum nudum* of various authors’), the second an *Oxalis*-

¹⁸ It should be emphasised that high-mountain grazing existed, at least in the Belianske Tatry Mts, towards the end of protohistoric times (for the Tatra region) already before Vlach pastoralism reached this region (Hoľub-Pacewiczowa 1931, Bohuš, 1972, 1994a).

¹⁹ E.g., *Atrichum undulatum*, *Brachythecium velutinum*, *Eurhynchium angustirete*, *Mnium spinosum*, *Plagiochila asplenioides*, *Plagiomnium undulatum*, *Rhizomnium punctatum*, *Thuidium abietinum* or *Brachythecium starkei*, *Dicranum scoparium*, *Hylacomium splendens*, *Plagiothecium curvifolium*, *Pleurozium schreberi*, *Polytrichum formosum*, *Rhytidiadelphus triquetrus* etc., and even *Sphagnum capillifolium*, *S. girgensohnii* (cf. Šmarda 1958, p. 47, Hadač et al. 1969, p. 277–280: rel. 225 (with *Acer pseudoplatanus* as codominant tree species) vs. the rest of relevés + p. 281–283 + p. 288 ff.; Šomšák 1986; Kučera 2012a, p. 287 ff. – selected relevés of substitute subanthropogenic Norway spruce stands).

-dominated woodland with more open *Picea* canopy and therefore better ecological conditions for development of field- and ground layer species.

The authors were of the opinion that their *Oxalis*-Norway spruce community approximately corresponds to '*Piceetum abietis oxalidetosum acetosellae silicicolum* Krajina 1933'. However, they changed this association name to the form '*Oxalido-Piceetum excelsae* Březina et Hadač, nomen novum' (Hadač et al. 1969, p. 270) to underline also the nomenclatural correctness of the name for this forest plant community as a separate association. Because the former association name was not validly published (see chapter 3.2.2.3 below), Březina et Hadač described a new association. [It should be highlighted that Šmarda (1966a, b)/Šmarda et al. (1971) classified the same *Oxalis*-Norway spruce community differently – as facies '*Sorbeto-Piceetum calcicolum* Pawłowski 1956 *oxalidetosum*', i.e. subassociation '*Sorbeto-Piceetum calcicolum* Šmarda et al. 1971 facies *oxalidetosum*'].

Hadač et al. (1969, p. 272–275) documented their '*Oxalido-Piceetum*' community of the Dolina Siedmich prameňov Valley with five phytocoenological relevés from altitudes of 1,350–1,510 m a. s. l. Slope inclination of the relevé sites is very steep (up to 51 °), the geological background consists of limestones, soils are rendzinas of (strongly acidic–) moderately acidic to neutral pH. [Hadač, Smola (1962b) also provided characteristics of snow cover in this and other woodlands of the studied territory.]

Similarly to the case of the above-discussed plant communities named after *Picea abies* and *Leucanthemum rotundifolium*, it was already earlier advised (cf. Kučera 2007 and subsequent works) to focus on the original description of the association '*Piceetum abietis oxalidetosum acetosellae silicicolum* Krajina 1933' – which represented the alliance '*Oxalidion acetosellae* Krajina 1933' in Krajina's (1933b) vegetation survey of the Mlynická dolina Valley – and likewise to the syntaxonomical content of the intended nomen novum '*Oxalido-Piceetum*' proposed by Březina and Hadač (Hadač et al. 1969, p. 270).

Contrary to the phytocoenological assessment of the stands of '*Chrysanthemo rotundifolii-Piceetum* sensu [Krajina 1933] Hadač et al. 1969 non Krajina 1933' from the Dolina Siedmich prameňov Valley (see chapter 3.2.1.2 above), relevés of '*Oxalido-Piceetum*' published by Hadač et al. (1969) represent a natural *Picea abies* woodland. There is no doubt about its classification within the class *Vaccinio-Piceetea* Br.-Bl. in Br.-Bl. et al. 1939, even though *Abies alba* should be naturally admixed in lower elevations of the vertical distribution of the latter association and the last relevé of Hadač et al. (1969, rel. 141) is considered to represent a secondary, artificially changed stand of former mixed montane *Fagus-Abies-Picea* forest of the class *Carpino-Fagetea* Jakucs ex Passarge 1968 (Kučera 2012a).

The above-mentioned habitat properties of the relevés published by Hadač et al. (1969) considerably differ from the ecological conditions of Krajina's stands of '*Piceetum abietis oxalidetosum acetosellae silicicolum* Krajina 1933' from the Mlynická dolina Valley (see above). The relevés of '*Oxalido-Piceetum abietis* Březina et Hadač in Hadač et al. 1969' [nom. corr., Art. 44] published originally by Hadač et al. (1969) also display substantially different floristic composition in comparison to Krajina's (1933b) phytocoenoses of '*Piceetum abietis oxalidetosum acetosellae silicicolum*'. Although physiognomically similar due to the dominance of *Oxalis acetosella* in the field layer, the phytocoenotic differences correspond to a completely different habitat quality of the respective *Oxalis*-

phytocoenoses within the Dolina Siedmich prameňov Valley. Statistical dissimilarities among the relevés under discussion, as well as their grouping, are depicted by their clustering pattern in the dendrogram (Fig. 7) and by their positions within the ordination diagram (Fig. 8)

The presented differential phytocoenological Table 2 (in Appendix) summarises the floristic differences between the two plant communities under consideration (*'Piceetum abietis oxalidetosum acetosellae silicicolum'* of Krajina [1933b] vs. *'Oxalido-Piceetum'* of Hadač et al. [1969]). In addition, the table is expanded with the original synoptic column of Sillinger's (1933) association *'Piceetum excelsae normale silicicolum'* Sillinger 1933' because Krajina (1933b, p. 154) synonymised his association with the latter unit. Further, two original relevés of *'Piceetum normale'* of Pawłowski et al. (1928) are added for comparison (cf. chapter 3.2.2.4 below). As in the preceding Table 1, less frequently occurring species in the respective community or species occurring in one of the four original communities are also included among the differential species because their occurrence or recorded cover-abundance scores are ecologically specific to the phytocoenoses of either Krajina, Hadač et al., Sillinger, or Pawłowski et al. as well. Chosen characteristics of the relevé plots are also attached.

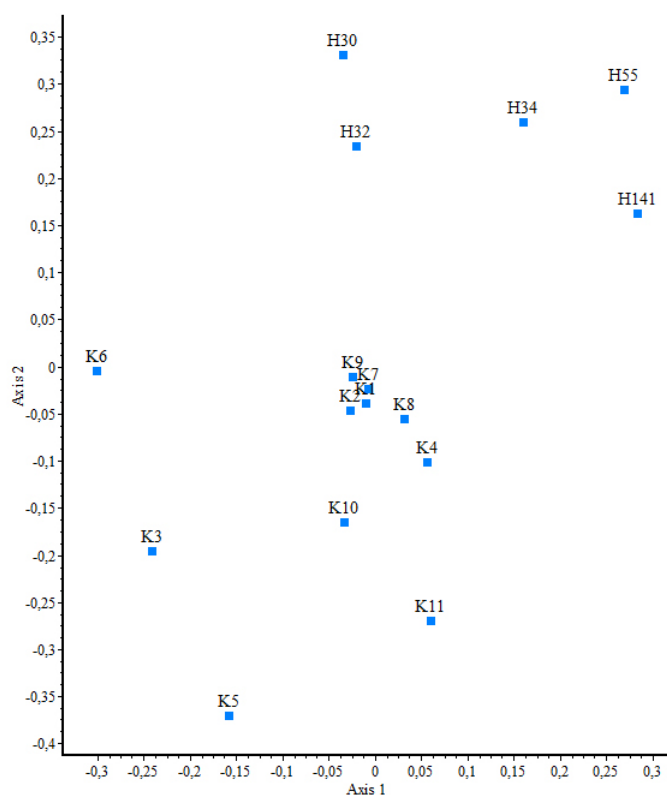
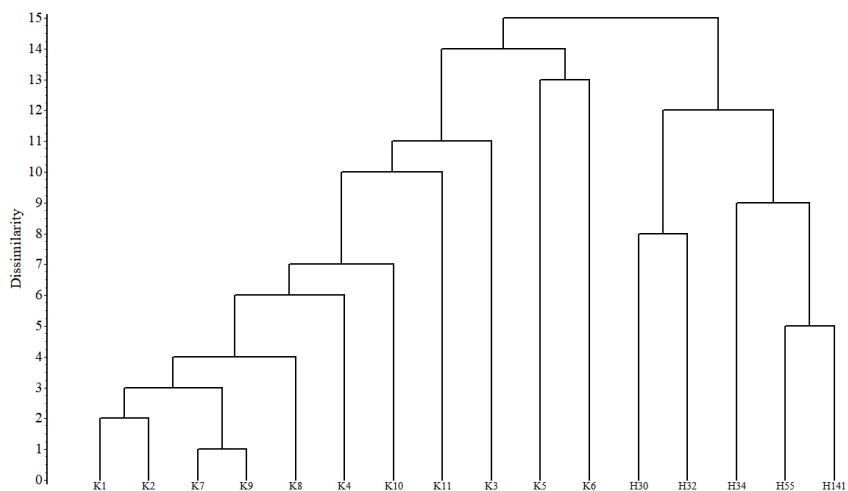
Occurrence of *Oxalis*-dominated field layer in the relevés *'Oxalido-Piceetum'* of Hadač et al. (1969) is probably partly induced by a higher cover of *Picea* trees, especially from earlier stages of stand development (Kučera 2012a), similarly to the case of Krajina's community. However, the absence of acidophiles (*Vaccinium vitis-idaea*, commonly also *Avenella flexuosa*, *Calamagrostis villosa*) and the presence of a nutrient-demanding species group (*Primula elatior*, *Myosotis sylvatica*, *Astrantia major* and others) are clear differential attributes of stands of the Belianske Tatry Mts recorded by Hadač et al. (1969). Within the Norway spruce altitudinal vegetation zone of the Western Carpathians, such a plant species assemblage, although most commonly accompanied by calcicoles, constitutes the exclusive distinctive characteristics of natural calcareous *Picea abies* woodlands (cf. Kučera 2019, tab. 1 and Kučera 2022).

3.2.2.3 Nomenclatural and syntaxonomical consequences with summary

(I) Although Moravec in Jirásek (2002, p. 76) explicitly stated that the association name *'Piceetum abietis oxalidetosum acetosellae'* Krajina 1933'²⁰ was validly published, such nomenclatural evaluation does not correspond to Art. 3e of the current as well as the previous edition of the phytocoenological Code (Weber et al. 2000; Theurillat et al. 2021): the name is invalidly published. The intended replacement name *'Oxalido-Piceetum'* Březina et Hadač, nomen novum' (Hadač et al. 1969, p. 270) is therefore in fact a validly published new association name *'Oxalido-Piceetum excelsae'* Březina et Hadač in Hadač et al. 1969'.

All aspects of the floristical and ecological difference between the original relevés of the two discussed *Oxalis*-Norway spruce communities of Krajina (1933b) vs. Hadač et al. (1969), respectively, demonstrate justification of their classification as separate basic plant communities – syntaxonomically they do not represent the same association.

²⁰ The association name should be correctly cited as *'Piceetum abietis oxalidetosum acetosellae silicicolum'* Krajina 1933' – see the section under #1 below and Krajina (1933a, p. 800; 1933b, p. 145 and 154).



Figures 7 and 8. Grouping of the respective *Oxalis*-rich relevés of Krajina (1933b: “K”) and Hadač et al. (1969: “H”) according to hierarchical clustering (dendrogram) and ordination (scatter plot). For numbering see Tab. 1 in the Appendix.

Kučera (2007, 2010c/2012a) separated the respective syntaxa of Krajina (1933b) and Hadač et al. (1969) according to their general floristical affinities even at the level of the order within the class *Vaccinio-Piceetea* Br.-Bl. in Br.-Bl. et al. 1939 ('*Piceetalia excelsae*' vs. '*Athyrio filicis-feminae-Piceetalia*').

(II) Krajina (1933b) established for his association '*Piceetum abietis oxalidetosum acetosellae silicicolum* Krajina 1933' a new alliance '*Oxalidion acetosellae* Krajina 1933' (originally intended by him as a replacement name, see below). As reminded above, this form of the alliance name was later considered inadequate for respective *Picea abies*-dominated phytocoenoses therefore Hadač (1962) published the replacement name '*Oxalido-Piceion* (Krajina 1933) Březina et Hadač in Hadač 1962'.

However, the floristical and ecological characteristics of the alliance '*Oxalido-Piceion*' given by Hadač et al. (1969, p. 265 ff.) – specified by the included associations '*Mnio spinosi-Piceetum*' and '*Oxalido-Piceetum excelsae* Březina et Hadač' – does not correspond to syntaxonomical content of the original name '*Oxalidion acetosellae* Krajina 1933 nom. illeg.' (≡ '*Oxalido-Piceion* (Krajina 1933) Březina et Hadač in Hadač 1962') as defined by Krajina (1933b).

This means that original relevés of Hadač et al. (1969) from either '*Oxalido-Piceetum excelsae*' or '*Mnio spinosi-Piceetum*' do not syntaxonically belong to the alliance '*Oxalido-Piceion* (Krajina 1933) Březina et Hadač in Hadač 1962'. The respective alliance name utilised by Hadač et al. (1969) has to be therefore labelled as a pseudonym – '***Oxalido-Piceion sensu Hadač et al. 1969 non (Krajina 1933) Březina et Hadač in Hadač 1962***'.

This pseudonymical phytocoenological content was followed by all later Slovak authors up to the present (cf. Jarolímek et al. 2008), except for Kučera (2007, 2010a, [2012a]) who proposed to recognising only the name '*Oxalido-Piceion* Hadač et al. 1969' as the first valid publication of the respective form of this name. However, such nomenclatural assessment is incorrect (see chapter 3.2.2.4 below). Diverse use of the alliance name '*Oxalido-Piceion*' – either as a correct name, partially without reflection of its whole syntaxonomical content (see below), or as a pseudonym – resulted in various nomenclatural and syntaxonomical use of the name in the literature.

(III) The presented case of differences between the *Oxalis*-Norway spruce community of Krajina (1933b) and that of Hadač et al. (1969) has four nomenclatural and syntaxonomical consequences:

A) Krajina's original relevés of the association '*Piceetum abietis oxalidetosum acetosellae silicicolum* Krajina 1933' represent a floristically and ecologically independent woodland plant community,²¹ however, distinct from the association '*Oxalido-Piceetum* Březina et Hadač in Hadač et al. 1969'.

B) In contrast to the above-presented *Chrysanthemum*-alliance names, the proposal to rename the alliance '*Oxalidion acetosellae* Krajina 1933' to the form '*Oxalido-Piceion* (Krajina 1933) Březina et Hadač in Hadač 1962' was nomenclaturally adequate (Art. 29b).

C) However, the association '*Oxalido-Piceetum* Březina et Hadač in Hadač et al. 1969' does not belong to the alliance '*Oxalido-Piceion* (Krajina 1933) Březina et Hadač in Hadač 1962' because Hadač et al. (1969) used this alliance name as a pseudonym

²¹ Currently classified within the association *Lophozio-Piceetum* Volk in Br.-Bl. et al. 1939 (Kučera 2023).

– i.e. ‘*Oxalido-Piceion* sensu Hadač et al. 1969 non (Krajina 1933) Březina et Hadač in Hadač 1962’.

D) In the need for a name replacing the pseudonym ‘*Oxalido-Piceion* auct. non (Krajina 1933) Březina et Hadač in Hadač 1962’ as well as the pseudonym ‘*Chrysanthemo-Piceion* sensu Hadač et al. 1969 non (Krajina 1933) Březina et Hadač in Hadač 1962’ commonly used in European phytocoenological literature (see Introduction), Kučera (2019) mentioned the replacement with a new name ‘*Cortuso-Piceion*’. This alliance name was proposed almost 20 years ago already; however, it was only recently formally validly published (Kučera 2007, 2022).

3.2.2.4 Other nomenclatural and syntaxonomical problems related to the alliance name ‘*Oxalido-Piceion*’

#1 – Nomenclatural and syntaxonomical ranking of the cited syntaxa and the syntaxonomical assessments of Krajina (1933b, p. 152–155) within his own chapter on the alliance ‘*Oxalidion acetosellae*’ are not fully consistent (cf. also Krajina 1933b, p. 215). For example, Krajina labelled his ‘Assoziation *Piceetum abietis oxalidetosum acetosellae silicicolum*’ also as a subassociation. This mostly results from ranks of the cited units of previous authors. Nevertheless, Krajina’s concluding evaluation was to attribute the rank of an association to this syntaxon.

As mentioned above, the name ‘*Piceetum abietis oxalidetosum acetosellae silicicolum* Krajina 1933’ was invalidly published (Art. 3e). This argument ultimately led Kučera (2007, 2010a) to the opinion that the superordinated alliance name ‘*Oxalidion acetosellae* Krajina 1933’ was likewise invalidly published (cf. Art. 8), and, that the subsequent replacement name ‘*Oxalido-Piceion* (Krajina 1933) Březina et Hadač in Hadač 1962’ was invalidly published as well.

However, such evaluation was incorrect: due to the confusing treatment of the description of the alliance ‘*Oxalidion acetosellae*’ by Krajina (1933b, p. 152–154), it was overlooked that the respective chapter contains two other published association names that could provide a sufficient original diagnosis of the alliance name ‘*Oxalidion acetosellae* Krajina 1933’ even though it might be disputed whether they represent the same syntaxon at all. These names belong to:

(A) Association ‘*Piceetum normale* (Pawłowski et al. 1928) Krajina 1933 nom. illeg.’ (Art. 34a) which originated from a change of rank of one subassociation of the properly cited original association ‘*Piceetum excelsae* [Pawłowski ex] Pawłowski et al. 1928’ (Krajina 1933b, p. 152).

(B) Association ‘*Piceetum excelsae normale silicicolum* Sillinger 1933 nom. illeg.’ (Art. 34a); this name was cited as a synonym to, in fact, a newly described association ‘*Piceetum abietis oxalidetosum acetosellae silicicolum* Krajina 1933’. Although such an assumed phytocoenological relation was not justified (see below [the paragraphs under section #3] and the Tab. 2) and the bibliographical citation of the page in Sillinger’s (1933) survey was mistaken, the name ‘*Piceetum excelsae normale silicicolum* Sillinger 1933’ also represents an element of the sufficient original diagnosis of the alliance ‘*Oxalidion acetosellae* Krajina 1933’.

#2 – Willner (2007, p. 239), and also Kučera (2007), pointed out that Krajina (1933b, p. 152) created the alliance name '*Oxalidion acetosellae*' as a replacement name for '*Piceion excelsae* Pawłowski 1928' (nom. inept., Art. 44) [i.e. *Piceion abietis* Pawłowski ex Pawłowski et al. 1928, nom. corr. (Art. 44)]. The hypothetical form and author citation of this name would be therefore '*Oxalidion acetosellae* (Pawłowski et al. 1928) Krajina 1933 nom. illeg.' (Art. 29b). Willner (2007, l. c.) subsequently stated that the name '*Oxalidion acetosellae*' is a homotypical synonym (Def. X) of '*Piceion excelsae* Pawłowski 1928'. This approach was repeated by Thébaud, Bernard (2018, p. 300).

Considering the syntaxonomical decision made previously by Krajina (1933b) as well as by Wallnöfer (1993), there is, however, a considerable conflict with the above-mentioned evaluation:

(A) The alliance '*Piceion abietis* Pawłowski ex Pawłowski et al. 1928 nom. corr.' was originally described with only one association '*Piceetum abietis* [Pawłowski ex] Pawłowski et al. 1928 nom. corr.' which comprised two subassociations – '*Piceetum normale* [Pawłowski ex] Pawłowski et al. 1928' (nom. illeg., Art. 13a, 34a) and '*Piceetum myrtilletosum* [Pawłowski ex] Pawłowski et al. 1928' (Art. 14b, 13b!). (Pawłowski et al. 1928, see p. 218 and also Kučera 2013).

For the purpose of conservation of the alliance name '*Piceion excelsae* Pawłowski in Pawłowski et al. 1928' with its traditional use as a syntaxon of acid Norway spruce woodlands, Wallnöfer (1993, p. 287) lectotypified the association '*Piceetum excelsae* Pawłowski in Pawłowski et al. 1928' with a relevé from its subassociation '*Piceetum myrtilletosum*'.

(B) In addition to this reasonable choice for the stability of syntaxonomical nomenclature, Krajina (1933b, p. 152–153) much earlier separated the above-mentioned subassociations of Pawłowski et al. (1928) into two separate alliances:

(1) subassociation '*Piceetum normale*', explicitly stated in the new rank as "... verbliebene Assoziation, das *Piceetum excelsae normale*" [= '*Piceetum excelsae normale* (Pawłowski et al. 1928) Krajina 1933 nom. illeg.'],²² to his '*Oxalidion acetosellae*' proposed as a new, however, illegitimate replacement name (Def. XIII, Art. 29b), and,

(2) subassociation '*Piceetum myrtilletosum*', for which the change of rank was not specified, to a new alliance '*Vaccinion myrtilli*' where it was cited as synonym within the subassociation *Vaccinietum myrtilli tatricum piceetosum abietis* (see Krajina 1933b, p. 145, 152, 180, 195).

It should be noticed that in nomenclatural terms, Krajina (1933b) frequently made a clear distinction between (1) the new names proposed by him and (2) the cited older names. One example illustrating this practice could be the way he cited '*Piceetum normale* Beger 1922' factually used by Szafer et al. (1923, p. 17) regardless of its common use under the label "*Piceetum normale* Szafer et al. 1923" (cf. also Braun-Blanquet et al. 1939, p. 23). Both names '*Piceetum abietis oxalidetosum acetosellae silicicolum*' and '*Oxalidion acetosellae*' lack an author citation; therefore, they should be ascribed to Krajina as new names.

²² It should be underlined that although Krajina (1933b, p. 152, 153) cited the name '*Piceetum normale*' of Pawłowski et al. (1928) in the text, he did not cite it as a synonym of '*Piceetum abietis oxalidetosum acetosellae silicicolum* Krajina 1933'.

(C) Following the later lectotypification designated by Wallnöfer (1993), the nomenclatural type of the alliance name given as '*Piceion excelsae* Pawłowski in Pawłowski et al. 1928' was consequently placed under Krajina's (1933b) new alliance '*Vaccinion myrtilli* Krajina 1933'. The alliance '*Oxalidion acetosellae*' of Krajina (1933b) therefore cannot be considered as a homotypical syntaxon to '*Piceion excelsae* Pawłowski ex Pawłowski et al. 1928'. The syntaxonomically and nomenclaturally more convenient approach is to treat the alliance '*Oxalidion acetosellae*' as a newly described name by Krajina (1933b) – an approach adopted by Hadač (1962) and all subsequent authors.

#3 – As mentioned above, it might be argued that the names '*Piceetum abietis oxalidetosum acetosellae silicicolum* Krajina 1933', '*Piceetum excelsae normale silicicolum* Sillinger 1933' and '*Piceetum normale* (Pawłowski et al. 1928) Krajina 1933' were meant – in Krajina's (1933b) terms – to represent one association. However, these three mentioned units do not represent the same plant community:

#3a – As explained before (chapter 3.2.2.1 above), Krajina's (1933b) own relevés of the alliance '*Oxalidion acetosellae* Krajina 1933', i.e. those within the association '*Piceetum abietis oxalidetosum acetosellae silicicolum* Krajina 1933 nom. inval.' (Art. 3e), should be divided into two groups: (1) a smaller subset representing acidic, more or less natural *Picea* woodlands of the alliance *Piceion abietis* Pawłowski ex Pawłowski et al. 1928 and (2) samples of anthropogenic forests mostly belonging to the order *Luzulo-Fagetalia* Scamoni et Passarge 1959.

#3b – Sillinger's (1933) phytocoenoses of the association '*Piceetum excelsae normale silicicolum* Sillinger 1933 nom. illeg.' (Art. 34a) [or forest type *Oxalis-Soldanella*] were described from middle montane altitudes of the Low Tatras situated in their eastern non-carbonate region, within the eastern one of the two proposed naturally beechless territories of the Low Tatras. They were assumed to reflect a conserved, older stage of postglacial vegetation development characterised by absence or only low presence of *Fagus sylvatica*.

However, it was centuries-long exploitation of forests which favoured *Picea abies* over *Abies alba*, *Fagus* and *Acer* spp. The community corresponding to the original description of '*Piceetum excelsae normale silicicolum* Sillinger 1933' represents (proto)historically altered phytocoenoses of the originally mixed *Fagus-Abies* forests (cf. Tab. 2, column III) (Kučera 2012a, b). They syntaxonomically belong to the class *Carpino-Fagetea* Jakucs ex Passarge 1968, within the group of mesic forests on mesotrophic non-calcareous soils.

#3c – Stands of altogether two relevés of '*Piceetum normale*' (cf. Pawłowski et al. 1928, tab. XII) were documented from an area with granitic bedrock (Nemčok et al. 1993), i.e. from non-carbonate habitats. This selected environmental characteristic is identical to the locus classicus of '*Piceetum abietis oxalidetosum acetosellae silicicolum* Krajina 1933'.

However, within the Western Carpathians, species populations of *Calamagrostis arundinacea*, *Fragaria vesca*, *Galeobdolon luteum* – as originally recorded within '*Piceetum normale*' of Pawłowski et al. (1928) are in woodlands on acidic rocks mostly found in lower montane altitudes, where mixed *Fagus-Abies* woodlands are – or were – native forest communities (cf. Walas 1933, tab. XVII, Sillinger 1933). Considering the location of the respective relevés and the centuries long exploitation of Tatras'

forests I regard the considered phytocoenoses of Pawłowski et al. (1928) as secondary, anthropogenic stands with an altered tree species composition. Moreover, the authors recorded their relevés on water-influenced habitats, “in the immediate vicinity of a stream” (Pawłowski et al. 1928, p. 258) what is indicated by presence of *Cardamine flexuosa*, *Chaerophyllum hirsutum*, *Chrysosplenium alternifolium*, *Myosotis sylvatica* as well as *Leucanthemum rotundifolium*.

The plant community ‘*Piceetum normale*’ of Pawłowski et al. (1928) phytocoenologically does not belong to either *Piceion abietis* Pawłowski ex Pawłowski et al. 1928 nom. corr. or to [calcicolous] ‘*Oxalido-Piceion* auct. non (Krajina 1933) Březina et Hadač in Hadač 1962’. Their relevés should be syntaxonomically assigned to the class *Carpino-Fagetea* Jakucs ex Passarge 1968, in the group of mesic forests on mesotrophic non-calcareous soils with subtle indication of habitat conditions close to communities of the mesotrophic water-influenced alliance *Stellario nemorum-Abietion albae* P. Kučera 2019 (? *Chaerophyllo hirsuti-Abietion albae* (Boeuf et al. 2014) Renaux et al. 2015 as a potential older heterotypic synonym).

#4 – Unlike most of the authors, Exner (2007) and Mucina et al. (2016) synonymised the alliance name ‘*Oxalido-Piceion excelsae* (Krajina 1933) Březina et Hadač in Hadač 1962’ with the name ‘*Piceion excelsae* Pawłowski et al. 1928’. Such classification originated from the second of two approaches to the former name (cf. also chapter 3.2.2.3 above) which are: (1) ‘*Oxalido-Piceion* auct. non (Krajina 1933) Březina et Hadač in Hadač 1962’ as calcicolous alliance of natural *Picea* woodlands, (2) ‘*Oxalido-Piceion* (Krajina 1933) Březina et Hadač in Hadač 1962’ as silicicolous alliance of natural *Picea* woodlands – this approach was possibly adopted also by Sýkora (1971) and partly by Jirásek (2002).

As explained above (section #4), the nomenclatural evaluation indicates that the alliance ‘*Oxalidion acetosellae* Krajina 1933’ (≡ ‘*Oxalido-Piceion* (Krajina 1933) Březina et Hadač in Hadač 1962’) may be lectotypified solely by one of the two following names: ‘*Piceetum normale* (Pawłowski et al. 1928) Krajina 1933’ or ‘*Piceetum excelsae normale silicicolum* Sillinger 1933’. This clarification is necessary because only these two names represent validly published elements of the original diagnosis. Such and restriction results from the fact that the name ‘*Piceetum abietis oxalidetosum acetosellae silicicolum* Krajina 1933’ is invalidly published.

Original diagnoses of the two former associations belong, however, to the class *Carpino-Fagetea* Jakucs ex Passarge 1968 (see section #3). This means that neither of these associations can serve as a floristic or ecological basis for a syntaxon within the class *Vaccinio-Piceetea* Br.-Bl. in Br.-Bl. et al. 1969. Syntaxonomical placement of the alliance ‘*Oxalido-Piceion* (Krajina 1933) Březina et Hadač in Hadač 1962’ within the class *Vaccinio-Piceetea* Br.-Bl. in Br.-Bl. et al. 1969 as done by Exner (2007), Mucina et al. (2016) is therefore highly disputable.

3.2.3 *Athyrio-Piceetalia* Hadač 1962 vs. *Athyrio-Piceetalia* sensu Hadač et al. 1969

#5 – The issue of substantial floristical and ecological differences between the above analysed *Leucanthemum*- and *Oxalis*-Norway spruce communities described by Krajina (1933b) versus those of Hadač et al. (1969), respectively, was pointed out by Kučera (2007, 2010c/2012a). In my other work (Kučera 2010a) I disputed the validity of the name ‘*Athyrio-Piceetalia* Hadač 1962’ because, at that time, I evaluated this name as invalidly published due to the absence of the sufficient original diagnosis (sec. Art. 8). Following the then-presented nomenclatural conclusion, the name ‘*Athyrio-Piceetalia*’:

- would be validly published only later (cf. Hadač et al. 1969), therefore,
- its valid form would be ‘*Athyrio filicis-feminae-Piceetalia* Hadač ex Hadač et al. 1969’ (Rec. 10C), and, most importantly,
- its original diagnosis would substitute the common scientific use of the name ‘*Athyrio-Piceetalia* sensu auct. non Hadač 1962 in orig.’ (cf. Kučera 2012a).

The proposed name form ‘*Athyrio filicis-feminae-Piceetalia* Hadač ex Hadač et al. 1969’ was later applied by Mucina et al. (2016) in pan-European vegetation synopsis and they were followed by Škvorc et al. (2017), Dubyna et al. (2019) and Bergmeier (2020).

However, the proposal to evaluate the name ‘*Athyrio-Piceetalia* Hadač 1962’ as a nomen nudum (sec. Art. 2b, 8: Kučera 2010a) is nomenclaturally inadmissible – despite the minor inconsistencies found in Hadač’s (1962) synopsis, for example:

- the missing year after the citation of Krajina’s name ‘*Chrysanthemion rotundifolii*’, or,
- the bibliographic reference “BBC, LII.3”²³ apparently belonging to 1st part of Krajina’s survey (Krajina 1933a) only.

The required unambiguous reference (Art. 2b, Note 4) to the vegetation survey of Krajina (1933a+b) and thus to the names published by Krajina is indisputable. The two names ‘*Chrysanthemo-Piceion* (Krajina 1933) Březina et Hadač in Hadač 1962’ and ‘*Oxalido-Piceion* (Krajina 1933) Březina et Hadač in Hadač 1962’ as well as the superordinated name ‘*Athyrio-Piceetalia* Hadač 1962’ were therefore all validly published by Hadač (1962).

As explained in the previous subchapters, the common syntaxonomical application of the two last mentioned alliance names corresponds to very different habitats and distinct plant communities than those originally described by Krajina (1933b). Beginning with the monograph of Hadač et al. (1969), these names have been used as pseudonyms up to the present, nomenclaturally expressed as:

- ‘*Chrysanthemo-Piceion* auct. non (Krajina 1933) Březina et Hadač in Hadač 1962’, and,
- ‘*Oxalido-Piceion* auct. non (Krajina 1933) Březina et Hadač in Hadač 1962’.

The resulting nomenclatural evaluation of the order ‘*Athyrio-Piceetalia*’ is therefore identical: the generally accepted syntaxonomical application of the name contradicts its factual original diagnosis expressed with Krajina’s (1933b) alliances ‘*Chrysanthemion rotundifolii*’ and ‘*Oxalidion acetosellae*’. Beginning with Hadač et al. (1969), the order name is generally used as a pseudonym, i.e. as ‘*Athyrio-Piceetalia* auct. non Hadač 1962’.

²³ I. e.: *Beihefte zum Botanischen Centralblatt*, Band L [50], Zweite Abteilung [II] [therefore presumable form “LII”; or it is simply incorrect numbering], Heft 3.

In fact, already Hadač's (1962) own description of the order '*Athyrio-Piceetalia*' suggests a misinterpretation of the syntaxa established by Krajina (1933b): the original ecological characteristics of the order – "Mässig azidiphile bis subneutrophile Fichten- und Tannenwälder mit überwiegendem Hemikryptophytenunterwuchs" (Hadač 1962, p. 53) cannot be derived from Krajina's data and the respective descriptions (1933b, p. 145–161). Instead, such diagnosis could be deduced unequivocally from the field research of Březina & Hadač and coll. in the Belianske Tatry Mts (see Introduction, cited as #2 in the list of references of Hadač [1962]!), which at that time was still unpublished.

#6 – In addition to the highly recommended abandonment of Kučera's (2010a) proposal to reject the name '*Athyrio-Piceetalia* Hadač 1962', the remaining unresolved question of its factual syntaxonomical content should also be answered. As (1) the alliance name '*Abietion albae* Březina et Hadač in Hadač 1962' is a nomen nudum and (2) the alliance '*Chrysanthemo-Piceion* (Krajina 1933) Březina et Hadač in Hadač 1962 nom. illeg.' [= '*Chrysanthemion rotundifolii* Krajina 1933', the nomenclaturally correct name] was originally described for riparian and other similar *Leucanthemum rotundifolium* non-forest phytocoenoses of the non-carbonate High Tatras' habitats within supramontane (to alpine?) altitudinal vegetation zone, (3) the alliance '*Oxalido-Piceion* (Krajina 1933) Březina et Hadač in Hadač 1962' [= '*Oxalidion acetosellae* Krajina 1933 nom. illeg.'] remains as the exclusive source of the definition of the name '*Athyrio-Piceetalia* Hadač 1962' for its use as a *syntaxon of forest plant communities* [cf. also section #7 below].

As explained above, the elements of the original diagnosis of the alliance '*Oxalido-Piceion* (Krajina 1933) Březina et Hadač in Hadač 1962' represent mostly anthropogenic mixed *Picea abies* woodlands with *Abies alba* and *Fagus sylvatica*, which are appropriately classified within the class *Carpino-Fagetea* Jakucs ex Passarge 1968.

#6a – Woodlands of the class *Vaccinio-Piceetea* Br.-Bl. in Br.-Bl. et al. 1939 usually classified under the pseudonym '*Athyrio-Piceetalia* auct. non Hadač 1962', i.e. natural calcicolous *Picea abies* syntaxa of the highest forest altitudinal vegetation zone of European mountains, should be therefore placed under a different order name. Kučera (2019) proposed the replacement of the name '*Athyrio-Piceetalia* auct. non Hadač 1962' with the new name '***Cortuso matthioli-Piceetalia***'. This name was formally validly described in a subsequent paper (Kučera 2022).

Protection of the name '*Athyrio-Piceetalia* Hadač 1962' with a conserved type – a nomenclatural act established only within the newest edition of the phytocoenological Code (Art. 53) was not considered due to many years of the pseudonymous application of this name (basically from the beginning) and in respect to its inconsistent acceptance during the last decades.

#6b – Lectotypification of the name '*Athyrio-Piceetalia* Hadač 1962' utilizing the name '*Chrysanthemo-Piceion* (Kraj.) Březina et Hadač in Hadač 1962' as advertised by Thébaud, Bernard (2018) – i.e. correctly with the name '*Chrysanthemion rotundifolii* Krajina 1933' – would cause the syntaxonomical displacement of the order '*Athyrio-Piceetalia*' in the formation of non-forest vegetation, specifically within the class *Mulgedio-Aconitetea* Hadač et Klika in Klika 1944. Nevertheless, the name '*Athyrio-Piceetalia* Hadač 1962' was lectotypified by Jirásek (2002, p. 76) already with the alliance '*Oxalido-Piceion* (Krajina 1933) Březina et Hadač in Hadač 1962'.

#6c – Reflecting the lectotypification by Jirásek and taking into account the explanation in section #3 above, one possible solution would be to adopt a loose connection between the subassociation '*Piceetum normale* [Pawłowski ex] Pawłowski et al. 1928' (nom. illeg., Art. 13a, 34a) and the association '*Piceetum abietis oxalidetosum acetosellae silicicolum* Krajina 1933 nom. inval.' (Art. 3e) as given by Krajina (1933b, p. 154 [152]).

If one would consider these two units as the same syntaxon, this approach would facilitate the selection of a conserved type for the '*Piceetum normale* (Pawłowski et al. 1928) Krajina 1933' from Krajina's (1933b) relevés published within his Table 61, preferably from his relevés no. 5, 6 (or 11) (cf. chapter 3.2.2.1 above). This procedure would, ultimately, change the factual syntaxonomical application of the name '*Oxalido-Piceion* (Krajina 1933) Březina et Hadač in Hadač 1962' (cf. section #3 above) and the superordinated order name '*Athyrio-Piceetalia* Hadač 1962' as well. This act would, however, stand in direct conflict with the ecologically different original diagnosis of the subassociation '*Piceetum normale*' published by Pawłowski et al. (1928), exemplified by the presence of, e. g., *Cardamine flexuosa*, *Chaerophyllum hirsutum*, *Chrysosplenium alternifolium* etc. in their original relevés (cf. subsection #3c above).

Moreover, even such a type conservation would entail that the order name '*Athyrio-Piceetalia* Hadač 1962' becomes a heterotypical synonym of the order *Piceetalia abietis* Pawłowski ex Pawłowski et al. 1928 nom. corr.

3.2.4 Other associated nomenclatural and syntaxonomical issues

#7 – Mucina et al (2016, p. 32) evaluated the name '*Athyrio filicis-feminae-Piceetalia excelsae* Hadač 1962' as invalidly published according to Art. 2b. At the same time, they regarded its originally subordinated alliance names (Hadač 1962, p. 54) '*Oxalido-Piceion excelsae* (Krajina 1933) Březina et Hadač in Hadač 1962' and '*Chrysanthemo rotundifolii-Piceion* (Krajina 1933) Březina et Hadač in Hadač 1962' as validly published (cf. Mucina et al. 2016, p. 31, 32). This treatment is inconsistent because the superordinated order must in such a case be considered equally validly published (Art. 8) in Hadač's (1962) synopsis.

#7a – Moreover, it is disputable to complete the name '*Athyrio-Piceetalia* Hadač 1962' to the form '*Athyrio filicis-feminae-Piceetalia excelsae*' proposed by Mucina et al. (2016). Considering Hadač (1962) and the corresponding names of Krajina (1933b, tab. 60 and 61) there does not exist a reliable basis to make such a choice according to Rec. 10C.

#8 – Mucina et al. (2016), followed by Dubyna et al. (2019), listed the alliance name '*Athyrio alpestris-Piceion* Sýkora 1971' as a synonym under the accepted alliance name '*Chrysanthemo rotundifolii-Piceion* (Krajina 1933) Březina et Hadač in Hadač 1962' characterised as a group of "Mesic herb-rich spruce forests of the Central and Northern European mountains". Such treatment was published by Wallnöfer (1993) already.

However, the alliance '*Athyrio alpestris-Piceion* Sýkora 1971' is floristically and ecologically related to neither the the original syntaxonomical content of the name '*Chrysanthemo rotundifolii-Piceion* (Krajina 1933) Březina et Hadač in Hadač 1962 nom. superfl.' (≡ '*Chrysanthemion rotundifolii* Krajina 1933', see above) nor to the communities corresponding to the pseudonym '*Chrysanthemo-Piceion* auct. non (Krajina 1933) Březina et Hadač in Hadač 1962'.

In fact, the original diagnosis of the alliance '*Athyrio alpestris-Piceion* Sýkora 1971' – i.e. the association '*Athyrio alpestris-Piceetum* Hartmann ex Sýkora 1971 nom. illeg.' (Art. 31) – contains exclusively species-poor phytocoenoses of $\pm$ oligotrophic yet mesic habitats belonging to the association *Athyrio alpestris-Piceetum* Hartmann ex Hartmann et Jahn 1967. Due to their only minor floristical differences particularly against the association *Lophozio-Piceetum* Volk in Br.-Bl. et al. 1939, the alliance of Sýkora should be treated as a later synonym of the alliance name *Piceion abietis* Pawłowski ex Pawłowski et al. 1928 to which the latter unit belongs (Kučera 2010a, c, 2012a; Chytrý et al. 2013a).

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Abstrakt

Od čias vegetačnej štúdie *Die Pflanzengesellschaften des Tales „Dolina Siedmich prameňov“ in der Belaer Tatra* Hadača a kol. o rastlinstve juhovýchodnej časti Belianskych Tatier do súčasnosti, väčšina fytocenológov dôsledne používa meno radu '*Athyrio-Piceetalia* Hadač 1962' pre skupinu druhovo bohatých, zvyčajne karbonátových spoločenstiev smrečín. Popri mene tohto syntaxónu sa tiež používa jemu podradený zväz '*Chrysanthemo-Piceion* (Krajina 1933) Březina et Hadač in Hadač 1962' a – menej často – tiež zväz '*Oxalido-Piceion* (Krajina 1933) Březina et Hadač in Hadač 1962'. [Obe mená zväzov boli navrhnuté ako náhradné mená k názvom '*Chrysanthemion rotundifolii* Krajina 1933' and '*Oxalidion acetosellae* Krajina 1933']. Dôsledná revízia originálnych opisov oboch dotknutých zväzových mien na podklade terénneho výskumu v locus classicus oblasti skúmanej Krajinom však naznačuje, že ich zvyčajné syntaxonomické použitie nezodpovedá originálnym diagnózam. Terajšie (a zároveň dlhodobé) syntaxonomické poňatie mien týchto syntaxónov preto predstavuje ich názorné použitie v zmysle pseudoným – t. j. '*Chrysanthemo-Piceion* auct. non (Krajina 1933) Březina et Hadač in Hadač 1962' a '*Oxalido-Piceion* auct. non (Krajina 1933) Březina et Hadač in Hadač 1962'. Rovnako vedecké použitie mena ich nadradeného radu takisto predstavuje pseudoným – '*Athyrio-Piceetalia* auct. non Hadač 1962'. V príspevku sa uvádza stručný náčrt charakteristiky a prijatia diskutovaných mien v európskej literatúre, nasledovaný detailným vysvetlením skutočnej originálnej charakteristiky a fytocenotického obsahu mien zväzov '*Chrysanthemo-Piceion* (Krajina 1933) Březina et Hadač in Hadač 1962' and '*Oxalido-Piceion* (Krajina 1933) Březina et Hadač in Hadač 1962'.

Kľúčové slová: fytocenologická nomenklatúra, lesné rastlinné spoločenstvá, *Picea abies*, rastlinné spoločenstvá, syntaxonómia, *Vaccinio-Piceetea*, Západné Karpaty.

Appendix

Table 1. Comparison of *Leucanthemum rotundifolium*-Norway spruce phytocoenoses of Krajina vs. Hadač et al.

All relevés are provided in the Domin cover-abundance scale.

	Krajina, 1933b, tab. 60						Hadač et al. 1969, p. 281–283			
Original relevé number	1	2	3	4	5	6	120	142	183	255
Relevé plot size (m ²)	80	300	40	30	15	6	100	100	30	45
Altitude a.s.l. (m)	1 430	1 450	1 505	1 510	1 530	1 545	1 275	1 325	1 250	1 260
Cover E ₃ (fraction or %)	2/3	1/4	1/4	3/4	1/2	3/4	75	60	70	65
Cover E ₂ (fraction or %)	–	–	–	–	–	2/3	–	–	–	–
Cover E ₁ (fraction or %)	1/1	1/1	1/1	1/1	9/10	5/6	70	80	70	80
Cover E ₀ (fraction or %)	2/3– 3/4	3/4	2/3– 3/4	1/2– 2/3	9/10	5/6	30	30	40	20
Tree and shrub species										
Canopy (E₃)										
<i>Picea abies</i>	4	2–3	3	6	4	3	7	7	8	8
<i>Pinus cembra</i>	.	.	.	.	+	1	.	.	.	.
<i>Sorbus aucuparia</i> ssp. <i>glabrata</i> *)	.	.	.	.	.	.	4	4	4	2
<i>Larix decidua</i> ssp. <i>polonica</i>	.	.	.	.	.	.	4	4	.	.
<i>Acer pseudoplatanus</i>	.	.	.	.	.	.	4	.	.	+
Understorey (E₂)										
<i>Pinus mugo</i>	.	.	+	.	.	2	.	.	.	.
<i>Lonicera nigra</i>	.	.	.	.	.	.	1	2	1	1
<i>Larix decidua</i> ssp. <i>polonica</i>	.	.	+	.	.	.	.	.	.	.
<i>Pinus cembra</i>	.	.	+	.	.	.	.	.	.	.
Field layer (E₁)										
<i>Ribes petraeum</i>	.	.	.	.	.	.	1	.	.	1
<i>Daphne mezereum</i>	.	.	.	.	.	.	1	.	.	.
<i>Picea abies</i>	.	+	.	.	.	.	.	.	.	.
Differential field layer species (E₁)										
<i>Viola biflora</i>	3	3	2–3	3	4	3–4	.	.	.	.
<i>Myosotis nemorosa</i>	3	2–3	4	1	1	1	.	.	.	.
<i>Alchemilla monticola</i>	2	2	4	+	2	2	.	.	.	.
<i>Aconitum firmum</i>	+	1	2	+	1	1	.	.	.	.
<i>Alchemilla glabra</i>	2	1	3	1	1	.	.	.	.	.
<i>Potentilla aurea</i>	2	1	2–3	.	+	.	.	.	.	.
<i>Vaccinium myrtillus</i>	+	+	.	.	+	+	.	.	.	.
<i>Senecio subalpinus</i>	4	4	3	3	2–3	1	.	1	.	1
<i>Chaerophyllum hirsutum</i>	+	3	1	2	2	.	.	.	.	2
<i>Ranunculus acris</i>	2	2	.	.	+	.	.	.	.	.
<i>Phleum rhaeticum</i>	+	.	1	.	.	.	.	.	.	.
<i>Hieracium caesium</i>	+	.	.	.	.	+	.	.	.	.
<i>Melampyrum sylvaticum</i>	.	+	+	.	.	.	.	.	.	.
<i>Deschampsia cespitosa</i>	.	.	1	+	.	.	.	.	.	.
<i>Agrostis stolonifera</i>	.	.	1–2	.	.	+	.	.	.	.
<i>Stellaria nemorum</i>	.	.	+	.	+	.	.	.	.	.
<i>Poa chaixii</i>	.	.	.	.	+	+	.	.	.	.
<i>Athyrium filix-femina</i>	.	.	.	.	.	.	5	4	6	5
<i>Dryopteris filix-mas</i>	.	.	.	.	.	.	5	4	5	2
<i>Myosotis sylvatica</i>	.	.	.	.	.	.	2	2	2	3

	Krajina, 1933b, tab. 60						Hadač et al. 1969, p. 281–283			
Original relevé number	1	2	3	4	5	6	120	142	183	255
<i>Galium schultesii</i>	.	.	.	.	.	.	1	2	1	2
<i>Epilobium montanum</i>	.	.	.	.	.	.	1	2	1	2
<i>Prenanthes purpurea</i>	.	.	.	.	.	.	1	2	2	1
<i>Pyrethrum clusii</i>	.	.	.	.	.	.	+	1	1	+
<i>Ranunculus lanuginosus</i>	.	.	.	.	.	.	1	3	.	3
<i>Actaea spicata</i>	.	.	.	.	.	.	2	1	4	.
<i>Cimicifuga europaea</i>	.	.	.	.	.	.	1	2	4	.
<i>Paris quadrifolia</i>	.	.	.	.	.	.	1	2	2	.
<i>Polygonatum verticillatum</i>	.	.	.	.	.	.	1	1	.	1
<i>Rubus idaeus</i>	.	.	.	.	.	.	2	1	.	1
<i>Petasites albus</i>	.	.	.	.	.	.	1	.	5	1
<i>Fragaria vesca</i>	.	.	.	.	.	.	2	.	1	1
<i>Mycelis muralis</i>	.	.	.	.	.	.	.	3	1	2
<i>Primula elatior</i> ssp. <i>tatrensis</i>	.	.	.	.	.	.	.	2	1	1
<i>Astrantia major</i>	.	.	.	.	.	.	.	2	2	1
<i>Senecio</i> 'nemorensis'*)	.	+	+	.	.	.	1	6	3	5
<i>Acetosa arifolia</i>	.	+	.	.	+	.	1	4	3	1
<i>Thalictrum aquilegifolium</i>	.	.	+	.	.	.	1	1	1	.
<i>Veratrum album</i> ssp. <i>lobelianum</i>	.	.	+	.	.	.	1	.	1	1
<i>Asarum europaeum</i>	.	.	.	.	.	.	1	.	1	.
<i>Dentaria glandulosa</i>	.	.	.	.	.	.	1	2	.	.
<i>Silene dioica</i>	.	.	.	.	.	.	1	1	.	.
<i>Anthriscus nitidus</i>	.	.	.	.	.	.	1	2	.	.
<i>Cirsium erisithales</i>	.	.	.	.	.	.	1	.	1	.
<i>Lilium martagon</i>	.	.	.	.	.	.	1	.	1	.
<i>Galeobdolon luteum</i>	.	.	.	.	.	.	.	2	2	.
<i>Hieracium murorum</i>	.	.	.	.	.	.	.	1	.	2
<i>Hieracium prenanthoides</i>	.	.	.	.	.	.	.	1	.	1
Other field layer species (E₁)										
<i>Leucanthemum rotundifolium</i>	7	9–10	5	8–9	8	7–8	5	5	4	4
<i>Oxalis acetosella</i>	3	2–3	+	+	2	2	3	4	5	6
<i>Gentiana asclepiadea</i>	2	+	1	1	1	2	2	1	1	1
<i>Phyteuma spicatum</i>	+	+	+	1	+	.	2	2	4	3
<i>Geranium sylvaticum</i>	+	2	1	.	+	+	1	2	.	1
<i>Soldanella carpatica</i> *)	+	+	+	1	1–2	3	.	.	.	.
<i>Soldanella carpatica</i> , <i>S. marmarossiensis</i> *)	.	.	.	.	.	.	.	2	.	2
<i>Calamagrostis villosa</i>	+	+	+	1	+	.	.	1	2	1
<i>Milium effusum</i>	+	+	.	.	+	.	2	2	3	.
<i>Hypericum maculatum</i>	+	+	+	.	.	.	2	1	.	.
<i>Homogyne alpina</i>	+	.	.	.	+	1–2	.	1	.	1
<i>Cicerbita alpina</i>	.	.	+	.	+	.	4	.	3	1
<i>Luzula sylvatica</i>	.	.	+	.	.	1	.	1	.	2
<i>Moneses uniflora</i>	1	r	.	.	.	.	.	.	3	.
<i>Coeloglossum viride</i>	.	2	.	.	+	.	1	.	.	.
<i>Valeriana excelsa</i> ssp. <i>sambucifolia</i>	.	+	.	.	.	.	2	2	.	.
<i>Doronicum austriacum</i>	.	+	.	.	.	.	1	.	4	.
<i>Valeriana tripteris</i>	.	+	.	.	.	.	.	.	1	3
<i>Solidago virgaurea</i> *)	.	.	+	.	.	+	.	.	.	1
<i>Gymnocarpium dryopteris</i>	+	1	.	.	.	.	.	.	.	.
<i>Adenostyles alliariae</i>	.	.	.	.	+	.	.	4	.	.

	Krajina, 1933b, tab. 60						Hadač et al. 1969, p. 281–283			
Original relevé number	1	2	3	4	5	6	120	142	183	255
<i>Luzula luzuloides</i>	.	.	.	.	.	+	+	.	.	.
<i>Dryopteris carthusiana</i>	.	.	.	.	.	.	1	.	1	.
<i>Ranunculus platanifolius</i>	.	.	.	.	.	.	+	1	.	.
<i>Crepis paludosa</i>	.	.	.	.	.	.	.	3	.	2
Differential ground layer species (E₀)										
<i>Rhytidiadelphus squarrosus</i>	2	2	4	1	1	2	.	.	.	.
<i>Mnium thomsonii</i>	2–3	1–2	1	2	6–7	4–5	.	.	.	.
<i>Brachythecium salebrosum</i>	1–2	2	3–4	3–4	1	+	.	.	.	.
<i>Brachythecium starkei</i>	3	2	.	+	.	.	.	.	.	.
<i>Cirriphyllum piliferum</i>	1	+	.	+	.	.	.	.	.	.
<i>Hylocomium pyrenaicum</i>	+	.	.	1	.	+	.	.	.	.
<i>Chiloscyphus polyanthos</i>	.	.	.	+	.	+	.	.	.	.
<i>Rhytidiadelphus triquetrus</i>	1	+	.	1	.	1	.	.	+	.
<i>Eurhynchium angustirete</i>	.	.	.	.	.	.	6	1	5	.
<i>Eurhynchium praelongum</i>	.	.	.	.	.	.	4	1	4	.
<i>Mnium spinosum</i>	.	.	.	.	.	.	3	5	.	5
<i>Brachythecium velutinum</i>	.	.	.	.	.	.	.	4	1	2
<i>Brachythecium oxycladum</i>	.	.	.	.	.	.	1	+	.	.
Other ground layer species (E₀)										
<i>Rhizomnium punctatum</i>	3	+	3	4	+	+	1	1	4	.
<i>Plagiomnium affine</i>	2	3–4	1	.	.	.	1	.	.	.
<i>Dicranum scoparium</i>	.	+	.	.	.	+	2	.	4	.
<i>Sanionia uncinata</i>	.	.	.	+	.	.	+	1	.	.
<i>Hylocomium splendens</i>	.	+	.	.	.	.	.	.	2	.

^{a)} See Krajina (1933b) and Hadač et al. (1969), respectively.

Other E₁ and E₀ species in one column only:

Krajina (1933b):

Rel. 1: E₁ – *Taraxacum* Sect. *Alpestris*^{a)} +; E₀ – *Peltigera canina* +.

Rel. 2: E₀ – *Barbilophozia hatcheri* +.

Rel. 3: E₁ – *Cerastium fontanum* +, *Leontodon hispidus* +, *Luzula sudetica* +, *Prunella vulgaris* +, *Ranunculus repens* +; E₀ – *Bryum weigelii* 2, *Marchantia polymorpha* ssp. *montivagans*^{a)} 2, *Scapania undulata* 2.

Rel. 4: E₁ – *Alchemilla incisa* +, *Caltha palustris* ssp. *laeta* +; E₀ – *Brachythecium reflexum* +, *Scapania subalpina* +.

Rel. 5: E₀ – *Barbilophozia lycopodioides* +.

Rel. 6: E₁ – *Adoxa moschatellina* 2–3, *Avenella flexuosa* +.

Hadač et al. (1969)

Rel. 120: E₁ – *Aconitum variegatum* 1, *Ajuga reptans* 3, *Calamagrostis arundinacea* 1, *Chrysosplenium alternifolium* 2, *Dentaria bulbifera* 1, *Epilobium tetragonum* 1, *Hylotelephium argutum* 1; E₀ – *Dicranum montanum* 1, *Dicranoweisia crispula* 1, *Lepidozia reptans* 1.

Rel. 142: E₁ – *Dryopteris dilatata* 4, *Geranium phaeum* 1, *Geum rivale* 1, *Heracleum sphondylium* 1, *Pulmonaria obscura* 1, *Scrophularia scopolii* 1; E₀ – *Atrichum undulatum* 3, *Hypnum cupressiforme* +, *Plagiochila asplenoides* 1, *Plagiothecium denticulatum* 4.

Rel. 183: E₀ – *Eurhynchium schleicheri* 1, *Peltigera aphthosa* 1, *Plagiomnium undulatum* 2.

Rel. 255: E₁ – *Galeopsis speciosa* +, *Urtica dioica* 1, *Veronica officinalis* 1.

Table 2. Comparison of *Oxalis acetosella*-Norway spruce phytocoenoses of Krajina vs. Hadač et al. vs. Sillinger vs. Pawłowski et al.

The synoptic column of Sillinger (1933) is based on two relevés, the relevés of Pawłowski et al. (1928) are presented in the original Braun-Blanquet cover-abundance scale (e = taxon without a cover-abundance score). The remaining relevés are provided in the Domin cover-abundance scale.

	Krajina, 1933b, tab. 61														Hadač et al. 1969, p. 272-275	Sillinger, 1933, p. 78-80	Pawłowski et al. 1928, tab. XII
Original relevé number	1	2	3	4	5	6	7	8	9	10	11	30	32	34	55	141	1 (79) 2 (80)
Relevé plot size (m²)	120	400	500	100	800	300	100	100	100	2 000	54	100	150	100	100	100	4 500 1 500
Altitude a.s.l. (m)	1 355	1 370	1 400	1 400	1 450	1 500	1 300	1 360	1 365	1 375	1 475	1 500	1 510	1 470	1 400	1 350	1 000 and 1 340- 1 280
Cover E₃ (fraction or %)	6/5	1/1	3/4	9/10	9/10	9/10	2/3	2/3	1/2	6/7	2/3- 3/4	80	90	70	70	80	-
Cover E₂ (fraction or %)	0	+	+	+	0	1/5	+	0	+	1/10	+	3	2	0	0	0	-
Cover E₁ (fraction or %)	1/2	3/4	2/3	2/3- 3/4	4/5	3/4	5/6	9/10	1/1	1/1	3/4	90	95	50	50	40	-
Cover E₀ (fraction or %)	3/4	3/4	5/6	6/4	5/6	5/6	5/6	1/1	1/5- 1/4	1/1	9/10	50	40	40	50	30	-
Tree and shrub species																	
Canopy (E₃)																	
<i>Picea abies</i>	7	8-9	6-7	9	9	9	7	5	5	8-9	6	8	8	8	8	8	4-5 4-5
<i>Larix decidua</i> ssp. <i>polonica</i>	4	1-2	2-3	.	+	+	.	.	1	+	.	.	4	4	.	.	.
<i>Pinus cembra</i>	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.
<i>Sorbus aucuparia</i> ssp. <i>glabrata</i>	.	.	.	.	.	.	.	.	.	.	.	5	4	2	4	5	.
<i>Abies alba</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Fagus sylvatica</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Understorey (E₂)																	
<i>Lonicera nigra</i>	.	1	1	.	.	.	.	.	+	+	.	1	.	.	1	.	+
<i>Sorbus aucuparia</i> ssp. <i>glabrata</i>	.	+	+	.	.	.	+	.	.	+	.	1	2	.	.	.	+
<i>Sorbus aucuparia</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Picea abies</i>	.	.	+	+	.	2	.	.	.	2	+	.	.	.	.	.	.
<i>Pinus cembra</i>	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.
<i>Larix decidua</i> ssp. <i>polonica</i>	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.
<i>Ribes petraeum</i>	.	.	.	.	.	.	.	.	.	.	.	2	1	1	1	1	.
<i>Salix silesiaca</i>	.	.	.	.	.	.	.	.	.	.	.	+	1	.	.	.	+

	Krajina, 1933b, tab. 61											Hadač et al. 1969, p. 272–275					Sillinger, 1933, p. 78–80	Pawłowski et al. 1928, tab. XII	
Original relevé number	1	2	3	4	5	6	7	8	9	10	11	30	32	34	55	141	III	1 (79)	2 (80)
<i>Galeobdolon luteum</i>	.	.	.	.	.	.	.	.	.	.	.	2	.	.	2	.	2/2 (1–3)	+	+
<i>Polystichum lonchitis</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	.
<i>Astrantia major</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.
<i>Mycelis muralis</i>	.	.	.	.	+	.	.	.	.	.	.	.	.	1	3	2	1/2 (1)	.	.
<i>Senecio 'nemorensis'</i> ^{a)}	.	.	+	.	2	+	.	.	.	.	.	1	.	2	2	3	.	.	.
<i>Valeriana tripteris</i>	.	.	.	+	.	.	.	.	.	+	.	1	2	2	.	.	.	.	+
<i>Phegopteris connectilis</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2/2 (1–2)	+	+
<i>Milium effusum</i>	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	2/2 (1–2)	.	.
<i>Actaea spicata</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1/2 (1)	.	.
<i>Aegopodium podagraria</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1/2 (1)	.	.
<i>Ajuga reptans</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1/2 (1)	.	.
<i>Brachypodium sylvaticum</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1/2 (1)	.	.
<i>Dentaria glandulosa</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1/2 (1)	.	.
<i>Fragaria vesca</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1/2 (1)	.	+
<i>Neottia nidus-avis</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1/2 (1)	.	.
<i>Pulmonaria obscura</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1/2 (1)	.	.
<i>Senecio ovatus</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1/2 (1)	.	.
<i>Streptopus amplexifolius</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1/2 (1)	.	.
<i>Leucanthemum rotundifolium</i>	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	+	I
<i>Chrysosplenium alternifolium</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	+	+
<i>Cardamine flexuosa</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+
<i>Lycopodium annotinum</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+
<i>Calamagrostis arundinacea</i> ^{a)}	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	? I ^{a)}	? + ^{a)}
Other field layer species (E ₁)	6	5	4–5	6	7–8	7–8	3	2–3	3–4	3–4	2–3	8	8	7	7	6	2/2 (7–8)	.	.
<i>Oxalis acetosella</i>	2	3–4	5–6	2	+	+	+	2	1–2	5	2–3	4	4	.	.	.	2/2 (1–2)	2	2
<i>Vaccinium myrtillus</i>	3	3	3–4	2–3	+	+	6	7	4–5	6	5	2	3	.	.	.	2/2 (1–2)	I	3
<i>Homogyne alpina</i>	+	2	2	1	+	+	+	1	5	2	3	1	4	.	.	.	2/2 (1)	I	2
<i>Luzula sylvatica</i>	.	.	2–3	.	3	.	+	.	2–3	.	2–3	.	.	.	.	.	1/2 (1)	I	–I
<i>Soldanella marmarosiensis</i>	.	.	2–3	+	3	.	+	.	2–3	.	2–3	.	.	.	.	.	2/2 (4–5)	e	+
<i>Soldanella carpatica</i>	.	.	.	+	2	.	.	.	.	1	1–2	.	.	.	.	.	.	+	+

Original relevé number	Krajina, 1933b, tab. 61											Hadač et al. 1969, p. 272-275				Sillinger, 1933, p. 78-80	Pawłowski et al. 1928, tab. XII	
	1	2	3	4	5	6	7	8	9	10	11	30	32	34	55	141	1 (79)	2 (80)
<i>Soldanella marmarosensis</i> , <i>S. carpatica</i>	.	.	.	.	.	.	.	.	.	.	.	3	3	2	3	3	.	.
<i>Moneses uniflora</i>	+	.	+	+	+	+	+	.	+	.	.	1	2	1	2	.	.	+
<i>Hieracium murorum</i>	.	+	.	.	.	+	+	.	1	.	.	.	.	2	1	1	1/2 (1)	+
<i>Prenanthes purpurea</i>	.	+	1	.	.	.	+	.	.	.	.	1	2	.	1	4	2/2 (1-2)	.
<i>Luzula luzuloides</i>	.	+	+	+	.	.	+	+	1	.	.	.	.	.	1	.	1/2 (1)	+
<i>Solidago virgaurea</i> ^{a)}	.	+	+	+	.	.	.	.	1	.	.	1	+	1	.	.	.	.
<i>Polygonatum verticillatum</i>	1	.	1	.	.	.	.	.	+	.	.	.	.	1	1	.	2/2 (1)	+
<i>Cicerbita alpina</i>	.	.	+	.	+	.	.	.	.	.	.	2	+	.	1	.	2/2 (1)	.
<i>Phyteuma spicatum</i>	.	.	.	.	1	1	.	.	.	.	.	1	.	+	.	.	2/2 (1)	.
<i>Paris quadrifolia</i>	.	.	.	+	.	.	.	.	.	.	+	.	.	.	.	2	.	.
<i>Phyteuma spicatum</i>	.	.	.	.	+	.	.	.	.	.	+	1	.	.	.	.	1/2 (1)	e
<i>Doronicum austriacum</i>	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	+
<i>Rubus idaeus</i>	.	.	.	.	.	1	+	.	+	.	.	.	.	.	.	.	1/2 (1)	+
<i>Veronica officinalis</i>	+	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1/2 (1)	+
<i>Maianthemum bifolium</i>	.	2	1	.	.	.	.	.	.	.	.	.	.	.	.	.	2/2 (1)	.
<i>Acetosa arifolia</i>	.	.	+	.	.	1	.	.	.	.	.	.	.	.	.	.	.	e
<i>Adoxa moschatellina</i>	.	.	.	.	1	.	.	.	.	.	.	.	.	1	.	.	+	+
<i>Aconitum firmum</i>	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	+	+
<i>Veratrum album</i> ssp. <i>lobelianum</i>	.	.	.	.	+	.	.	.	.	.	.	+	.	.	.	.	.	.
<i>Viola biflora</i>	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	+
<i>Chaerophyllum hirsutum</i>	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	+
<i>Stellaria nemorum</i>	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	+
<i>Huperzia selago</i>	.	.	.	.	.	+	.	.	.	.	.	.	1	.	.	.	.	e
<i>Chamerion angustifolium</i>	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	+	+
<i>Pyrola minor</i>	.	.	.	.	.	.	.	.	.	.	+	1	.	.	.	.	.	.
<i>Ranunculus platanifolius</i>	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	2/2 (1)	.
<i>Clematis alpina</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1/2 (2-3)	.
<i>Epilobium montanum</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	+
<i>Petasites albus</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1/2 (1)	.

	Krajina, 1933b, tab. 61											Hadač et al. 1969, p. 272-275					Sillinger, 1933, p. 78-80	Pawłowski et al. 1928, tab. XII	
	1	2	3	4	5	6	7	8	9	10	11	30	32	34	55	141			
Original relevé number	1	2	3	4	5	6	7	8	9	10	11	30	32	34	55	141	III	1 (79)	2 (80)
Differential ground layer species (E₀)																			
<i>Rhytidadelphus triquetrus</i>	4	6	3-4	4	3	4-5	3	+	+	3	4-5	.	.	.	.	.	.	.	.
<i>Pleurozium schreberi</i>	1	2	2	2	.	2	4	1	+	5	2	.	.	.	.	.	.	2	2
<i>Brachythecium oedipodium</i>	1	.	1	4	.	.	.	3-4	.	2	.	.	.	.	.	.	.	.	2
<i>Plagiommium affine</i>	4	.	1	2-3	1-2	.	.	1	3	.	.	.	.	.	.	.	.	+	2
<i>Barbilophozia lycopodioides</i>	.	.	+	1	+	.	.	.	.	.	+	.	.	.	.	.	.	.	.
<i>Cetraria islandica</i>	.	.	+	+	+	.	.	.	.	1	+	.	.	.	.	.	.	.	.
<i>Hylacomium umbratum</i>	.	.	.	.	2	2	.	1	.	1	.	.	.	.	.	.	.	.	.
<i>Polytrichum commune</i>	.	.	2	1	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.
<i>Cladonia gracilis</i> var. <i>elongata</i> ^{*)}	.	.	+	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Barbilophozia hatcheri</i>	.	.	.	.	+	2	2-3	1	.	.	+	.	.	.	.	.	.	.	.
<i>Ptilium crista-castrensis</i>	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Polytrichum formosum</i>	2-3	.	.	.	3	1	1	4	.	3-4	.	1	.	.	.	.	.	2	2
<i>Sanionia uncinata</i>	.	.	1	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Cladonia chlorophaea</i>	.	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Mnium thomsonii</i>	.	.	.	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Rhytidadelphus squarrosus</i>	.	.	.	2	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.
<i>Polytrichum longisetum</i>	.	.	.	.	1	2-3	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Calypogeia suecica</i>	.	.	.	.	+	.	.	3	.	.	.	.	.	.	.	.	.	.	.
<i>Sphagnum girgensohnii</i>	.	.	.	.	.	.	.	2	.	3	.	.	.	.	.	.	.	.	.
<i>Cladonia furcata</i> f. <i>foliolosa</i> ^{*)}	.	.	.	.	.	.	.	.	.	1	+	.	.	.	.	.	.	.	.
<i>Plagiommium cuspidatum</i>	.	.	.	.	.	.	.	.	.	.	.	5	5	5	7	.	.	.	.
<i>Brachythecium velutinum</i>	.	.	.	.	.	.	.	.	.	.	.	.	4	2	1	.	.	.	.
<i>Plagiothecium sylvaticum</i> ^{*)}	.	.	.	.	.	.	.	.	.	.	.	2	.	2	.	.	.	.	.
<i>Rhizomnium punctatum</i>	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	+	.	.	.
<i>Mnium spinosum</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	5	.	.	.
<i>Mnium spinosum</i> , <i>M. spinu-</i> <i>losum</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	+
<i>Plagiothecium undulatum</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	+
<i>Dachiochila asplenoides</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	e	e

	Krajina, 1933b, tab. 61											Hadač et al. 1969, p. 272–275					Sillinger, 1933, p. 78–80	Pawłowski et al. 1928, tab. XII	
Original relevé number	1	2	3	4	5	6	7	8	9	10	11	30	32	34	55	141	III	1 (79)	2 (80)
Other ground layer species (E ₀)																			
<i>Dicranum scoparium</i>	2–3	3	3	+	+	2	2	2–3	.	3	1	6	4	3	3	1	.	.	.
<i>Hylacomitrium splendens</i>	3	3	+	3	+	3	5	.	+	5	2	3	3	2	1	.	.	3	2–3
<i>Ptilidium ciliare</i>	.	.	.	.	.	+	.	.	.	.	.	+	1	.	.	.	.	.	.
<i>Plagiothecium denticulatum</i>	.	.	.	.	.	.	.	1	.	.	.	.	.	.	4	1	.	.	.
<i>Cirriophyllum piliferum</i>	.	.	+	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.
<i>Blepharostoma trichophyllum</i>	.	.	.	.	.	.	.	+	.	.	.	1	.	.	.	.	.	.	.
<i>Sphagnum capillifolium</i>	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	+

*) See Krajina (1933b) or Hadač et al. (1969) or Pawłowski et al. (1928), respectively.

Other E₁ and E₀ species in one column only:

Krajina (1933b):

Rel. 3: E₁ – *Hieracium caesium* +, *H. carpathicum* +; E₀ – *Cladonia digitata* +, *C. squamosa* +, *C. ochrochlora* +.

Rel. 4: E₀ – *Sphagnum majus* 1.

Rel. 5: E₁ – *Hylotelephium argutum* +, *Myosotis nemorosa* +, *Senecio subalpinus* 1, *Valeriana excelsa* ssp. *sambucifolia* +; E₀ – *Bazzania tricenata* +, *Brachythecium rivulare* 1, *Plagiochila asplenoides* +.

Rel. 6: E₁ – E₀ – *Cladonia deformis* +, *C. subsquamosa* +, *Dibaeis bacomyces* +, *Polytrichum juniperinum* +, *Sphagnum fimbriatum* 1,

Rel. 10: E₀ – *Peltigera aphthosa* 1, *P. polydactyla* 2.

Rel. 11: E₁ – *Pseudorchis albida* +; E₀ – *Jamesoniella autumnalis* +.

Hadač et al. (1969):

Rel. 30: E₀ – *Brachythecium glareosum* 2, *Eurhynchium schleicheri* 2.

Rel. 32: E₁ – *Orthilia secunda* 1; E₀ – *Plagiothecium curvifolium* 4.

Rel. 34: E₁ – *Anthriscus nitidus* 1, *Cardaminopsis borbassii* 1, *Pyrethrum clusii* 1.

Rel. 55: E₁ – *Asarum europaeum* 1, *Galium schultesii* 1, *Ranunculus repens* 1.

Rel. 141: E₀ – *Eurhynchium praelongum* 1, *Peltigera canina* 1.

Pawłowski et al. (1928):

Rel. 1 (79): E₁ – *Circaeae alpinae* e, *Alchemilla palmata* +, *Blechnum spicant* +, *Carex digata* +; E₀ – *Isoetecium myurum* e.

Rel. 2 (80): E₁ – *Coeloglossum viride* e, *Crepis paludosa* e, *Cystopteris fragilis* +, *Deschampsia cespitosa* e, *Listera cordata* +.

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