

## Natural acid Norway spruce woodlands in Slovakia and their syntaxonomical classification along with selected problems of syntaxonomical delimitation of the order *Piceetalia abietis* in Europe

Peter Kučera

**Summary:** A second version of the syntaxonomical classification of acid Norway spruce communities is presented for the region of Slovak Western Carpathians based on the recent knowledge on delimitation of natural Norway spruce woodlands in Slovakia. As a result, two in Slovakia traditionally recognized associations are distinguished: *Lophozio-Piceetum* Volk in Br.-Bl. et al. 1939 (syn. *Calamagrostio villosae-Piceetum* auct. non Schlüter 1966) as the most wide-spread, however, only negatively differentiated community, and *Athyrio distentifolii-Piceetum* Hartmann ex Hartmann et Jahn 1967 in more humid habitats which allow *Athyrium distentifolium* domination and richer species abundance. The statistical synthesis also supported differentiation of new separate associations ecologically and/or chorologically bound to habitats limited to high mountain ranges only – as, for example, associations *Solidagini virgaureae-Piceetum* and *Parido quadrifoliae-Piceetum*. *Listero cordatae-Piceetum abietis* is described for unique scree phytocoenoses, while *Lycopodio annotini-Sorbetum* comprises special types of secondary successive (partly scree) phytocoenoses. A marginal position in the group of natural acid Norway spruce communities has the association *Sphagno capillifolii-Piceetum abietis* Zukrigl 1973 nom. corr. which is distinguished by the occurrence of bog species. Notes on the possible occurrence of the association *Dryopterido dilatatae-Piceetum* are added as well. Nomenclatural and syntaxonomical comments on the associations *Bazzanio-Piceetum* (Schmid et Gaisberg 1936) Br.-Bl. et Sissingh in Br.-Bl. et al. 1939 nom. corr., *Luzulo sylvaticae-Piceetum* Wraber 1963, *Homogino alpinae-Piceetum* Zukrigl 1973 etc. are given in detail. Syntaxonomical delimitation of taiga woodland of northern East European to Siberian region with *Picea obovata* and *Abies sibirica* is proposed.

**Keywords:** acid plant community, forest plant community, nomenclature, *Picea abies*, *Piceetalia abietis*, *Piceo obovatae-Abietetea sibiricae*, phytocoenology, supramontane woodland, syntaxonomy, *Vaccinio-Piceetea*, Western Carpathians

Communities of the class *Vaccinio-Piceetea* Br.-Bl. in Br.-Bl. et al. 1939 split into two cardinal subordinated units which differ in their floristical composition and ecological properties: (1) usually species-poor communities growing on (very) strongly acidic soils, i.e. distributed over non-carbonate rocks and (2) species-rich communities growing on moderately to slightly acidic and neutral soils, i.e. inhabiting areas of various carbonate rocks. Since the syntaxonomical overview of HADAČ (1962) these two units are classified in the rank of an order and even if some later authors did not accept that syntaxonomical rank, their statistical syntheses nevertheless revealed the respective two cardinal units (cf. EXNER et al. 2002; JUVAN et al. 2013). This differentiation is valid on supraregional to continental scale. These two orders are traditionally labelled as *Piceetalia excelsae* Pawłowski ex Pawłowski et al. 1928 and *Athyrio-Piceetalia* Hadač 1962; however, the latter name should be replaced for nomenclatural reasons (KUČERA 2023) by another name: KUČERA (2022) proposed the name *Cortuso matthioli-Piceetalia* P. Kučera 2022.

Natural Norway spruce communities of both these groups are represented in the Western Carpathians. For the territory of Slovakia, two syntaxa checklists of the class *Vaccinio-Piceetea* have been published up to the present: (1) Šomšák's list of syntaxa (in MUCINA et al. 1985) based

mostly on studies of HADAČ et al. (1969), ŠOLTÉS (1976) and FAJMONOVÁ (1978) and (2) recent derived checklist of JAROLÍMEK et al. (2008a).

Altogether three associations of natural acid Norway spruce communities were traditionally differentiated: *Vaccinio myrtilli-Piceetum* Šoltés 1976 (syn. *Calamagrostio villosae-Piceetum* auct. non Schlüter 1966) within the alliance *Piceion excelsae* Pawłowski ex Pawłowski et al. 1928, *Athyrio alpestris-Piceetum* Hartmann ex Hartmann et Jahn 1967 assigned to a separate alliance *Athyrio alpestris-Piceion* Sýkora 1971 as well as '*Chrysanthemo rotundifolii-Piceetum* sensu Krajina 1933 non auct.' within the alliance *Chrysanthemo-Piceion* sensu Krajina 1933 non (Krajina 1933) Březina et Hadač in Hadač 1962 (cf. KUČERA 2012a, 2023).

KUČERA (2012a) published a commented overview of distribution of the Norway spruce woodland in the territory of the Western Carpathians, associated with a revision of traditional views on their natural distribution. An important part was the first comprehensive syntaxonomical revision of the natural supramontane Norway spruce syntaxa of Slovakia.

Aim of this paper is presenting updated syntaxonomical classification and nomenclatural revision of natural acid Norway spruce communities found in the territory of the Western Carpathians in Slovakia. The preceding syntaxonomical revisions of the class *Vaccinio-Piceetea* were dedicated to syntaxonomy of Arolla pine communities (KUČERA 2017, 2019a), natural calcareous Norway spruce communities (KUČERA 2022) and coniferous wet woodland communities (KUČERA 2019b, with exception of bog woodland communities).

## Materials and methods

This contribution presents partial results of the syntaxonomical revision of the communities of the class *Vaccinio-Piceetea* Br.-Bl. in Br.-Bl. et al. 1939 present in Slovakia, originally intended to be part of the specialized volume of the 'Rastlinné spoločenstvá Slovenska' (1995–2022) on the forest and scrub vegetation (VALACHOVIČ et al. 2022). Therefore the presented relevé dataset selection follows the methodical directions established for that monograph:

- (1) The dataset for Slovak forest and scrub phytocoenoses was officially closed to the date 27.5.2016 and no newly published relevés were accepted. According to this regulation, numerous relevé data of Arolla pine woodland published by ZIĘBA et al. (2018) were not included in the statistical comparisons of the *Vaccinio-Piceetea* alliances in this work. The final dataset was exported from Slovak vegetation database (ŠIBÍK 2012; <https://www.givd.info/ID/EU-SK-001>) by J. Šibík (Institute of Botany SAS, Bratislava), as it was made available to the respective authors of chapters on Slovakian forest and scrub vegetation.
- (2) For forest communities only relevés with plot sizes 200–650 m<sup>2</sup> were accepted. We adhered to this regulation even if some typical relevés with sizes between 100–200 m<sup>2</sup> would have been omitted in this study.
- (3) Selected taxa were merged to species aggregates such as *Dryopteris carthusiana* agg.,<sup>1</sup> *Senecio nemorensis* agg. or to the nearest mutual taxonomical rank (e.g. *Solidago virgaurea* ssp. *minuta* + *Solidago virgaurea*) or united within a taxonomically more appropriate name (e.g. *Ranunculus*

<sup>1</sup> Only species *D. carthusiana* and *D. dilatata* were traditionally distinguished within the studied forest stands. However, also *D. expansa* is the native component of the natural *Picea abies* woodlands in the Western Carpathians (cf. KUČERA 2012a) along with various hybrids (Tatra Mountains, Kučera, not.)

*aconitifolius* included into *R. platanifolius* or *Soldanella hungarica* + *S. montana* + *S. hungarica* ssp. *major* into *S. marmorossiensis* agg.).

The resulting dataset was stored in Turboveg for Windows database software (HENNEKENS 1998–2020) (cf. HENNEKENS & SCHAMINÉE 2001) and selection of *Vaccinio-Piceetea* phytocoenoses with respect to above-mentioned limitations was performed by the author. Some of the relevés were revised according to originally published data.

In respect of the thorough revision of literature sources, records of explicit successional stages (e.g. some relevés of KRAJINA 1933) as well as relevés with missing ground layer species were excluded. Relevés of phytocoenoses with natural occurrence of *Pinus cembra* were also excluded, because they are classified within the alliances *Calamagrostio variae-Pinion cembrae* and *Homogyno alpinae-Pinion cembrae* (cf. KUČERA 2017). With regard to different floristical patterns of calcareous and acid Norway spruce woodlands (cf. KUČERA 2012a), the set of acid phytocoenoses was separated.

In attempt to maximize quality of data selected for statistical classification of Slovak *Picea abies* phytocoenoses of the Western Carpathians, the available relevé data were thoroughly re-analysed with regard to revisions of the natural distribution of *Picea abies* communities in Slovakia (see below). The most important part is to eliminate potential data contamination with floristical and ecological influence of anthropogenically degraded forest communities, especially exclusion of data recorded in unequivocally identified substitutionary Norway spruce stands (see below in chapter ‘Results’, for the detailed explanation see KUČERA 2012a).

As a result, a strict restriction of altitudinal limit was adopted: relevé data from localities below an elevation of 1400 m a.s.l. were excluded. This subjective decision is based on field observations of *Fagus* and mixed *Fagus* woodland stands found above 1300 m a.s.l. on expositions of all four cardinal directions, with emphasis on the preserved *Fagus* stands reaching with their artificially lowered upper forest line (!) above 1340–1350 m a.s.l. on non-carbonate bedrock. In the carbonate regions such artificial upper forest line of mixed *Fagus* woodland of the class *Carpino-Fagetea* above 1360–1390 m a.s.l. was confirmed in the field.

Below the chosen altitudinal limit (1400 m a.s.l.) only carefully selected relevés of *Picea abies* phytocoenoses were accepted for the dataset. They represent plant communities mostly found on ecologically more extreme habitats which hinder development of the *Carpino-Fagetea* plant communities, within the Western Carpathians, for example, on screes and other stony accumulations, i.e. such habitats which support an extragradal occurrence of natural acid Norway spruce phytocoenoses (cf. the association *Listero cordatae-Piceetum* with relict *Linnaea borealis* occurrences).

No other phytocoenological relevés were eliminated at this stage of data preparation, even if they represented untypical of problematically identifiable phytocoenoses. The complete list of used relevés is summarily presented by KUČERA (in red.), see also below the particular associations.<sup>2</sup>

The subfinal dataset with 133 relevés was exported to the software package JUICE (TICHÝ 1998–2020; cf. TICHÝ 2002) for further modification, especially merging of taxa (see above) and, subsequently, exported for statistical analysis performed by the software package SYN-TAX 2000

<sup>2</sup> In comparison to the dataset used for acid Norway spruce communities by KUČERA (2019b, tab. 1: ‘135 relevés’), two relevés were removed (and included into the dataset of *Cortuso-Piceetalia* phytocoenoses, KUČERA 2022): KOBZÁKOVÁ (1987), tab. 8, rel. 7; MIADOK (1995): 60, rel. 2.

(PODANI 2001a). The ordinal hierarchical clustering was executed to evaluate also quantitative information provided by ordinal Braun-Blanquet's scale (cf. KUČERA 2011a) and the Podani's discordance coefficient was used as it takes into account also presence vs. absence relation (PODANI 2001b).

During the performed data analyses, it was revealed that developmental stages, for example with increased *Sorbus aucuparia* presence, could significantly influence the statistical classification and as a result, *S. aucuparia*-pseudocommunities were produced without having other sufficient diagnostic floristical attributes. Anthropogenic influence on *Larix decidua* presence could also influence the data classification. Further SYN-TAX 2000 classifications were therefore performed on dataset with field ( $E_1$ ) and ground layer ( $E_0$ ) species only.

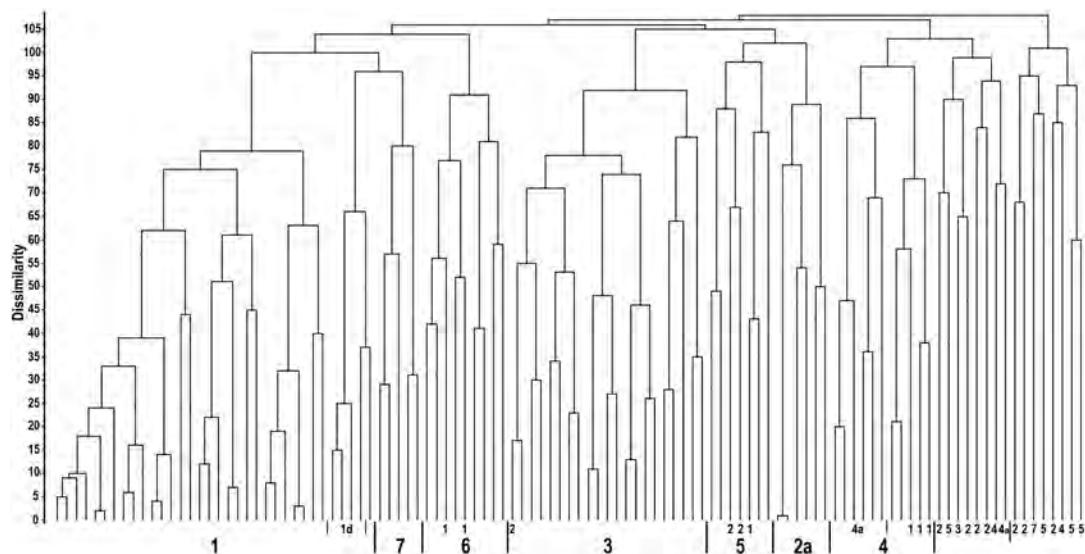
Another detected source of dataset pseudo-variability was most probably an intentional omission of any data on bryophyte species presence as well as ground layer cover in Norway spruce relevés of MIADOK (1995). Their inclusion in the statistical classification – together with peculiar data on *Soldanella* taxa cover-abundances – resulted in the creation of pseudo-syntaxa made of MIADOK's (1995) relevés. The respective relevés should not be treated as real non-moss phytocoenoses, instead, they should be assessed as data with missing information on the ground layer. As a result, all 21 remaining relevés of MIADOK (1995) were removed from the dataset.

Finally, three relevés of KANKA (2008: tab. 9, rel. 8; tab. 9, rel. 12; tab. 16, rel. 10) were removed because they, in fact, represent Norway spruce communities ecologically and floristically influenced by carbonate rocks, therefore they should be classified as *Cortuso-Piceetalia* phytocoenoses.

For all the above-mentioned reasons, the final dataset consists of 109 relevés only. The final relevé classification is based on statistical classification of data on the field layer ( $E_1$ ) species – presented within the resulting dendrogram in the Fig. 1. However, subjective manual re-adjustment of some relevés was applied in order to achieve floristically and ecologically more compact units – especially considering the pre-final statistical classification which included also the ground layer ( $E_0$ ) species (cf. below *Lycopodio annotini-Sorbetum*): most frequently from the heterogeneous group of non-typical relevés which were not excluded from the statistical classification (cf. Fig. 1).

The differential attributes of the respective syntaxa (fidelity and frequency values) and resulting tables were elaborated within JUICE; the concept of fidelity was used (CHYTRÝ et al. 2002a). Fidelity calculations ( $\phi$ -values) are based on the presence/absence data with a standardization of relevé groups to an equal size. Performing the Fisher's exact test, zero fidelity was given to species with significance  $P > 0.05$  in a particular cluster (TICHÝ & CHYTRÝ 2006).

The formal sequence of species groups in Table 1 is adjusted according to the template of differential tables of the Vegetation of the Czech Republic, Vol. 4 (CHYTRÝ et al. 2013a), i.e. trees, shrubs, differential and other species of the field and ground layer separately; constancy and fidelity values equal and higher than 50 are highlighted in boldface type. Statistically determined diagnostic species are ranked according to fidelity values. The conventional levels of statistical significance (0.05, 0.01 and 0.001, Fisher's exact test) for the particular species are indicated with asterisks (\*, \*\*, \*\*\*). Due to low total number of available natural Norway spruce relevés as well as very low total number of species within some associations, species with the lowest diagnostic value ( $\phi$ -value  $\geq 0.25$  at Fisher's exact test 0.05-limit) were also retained as 'diagnostic species' for individual syntaxa, bearing in mind their availability for future comparisons and potential use during field research.



**Figure 1.** Dendrogram of the ordinal hierarchical clustering of the relevés of natural acid *Picea abies* communities from Slovakia. 1 – *Lophozio-Piceetum abietis*; 1d – *Lophozio-Piceetum polytrichetosum communis*; 2 – *Athyrio distentifolii-Piceetum abietis*; 2a – *Athyrio distentifolii-Piceetum abietis*, more typically developed relevés; 3 – *Solidagini virgaureae-Piceetum abietis*; 4 – *Parido quadrifoliae-Piceetum abietis*; 4a – *Parido quadrifoliae-Piceetum abietis*, typical stands; 5 – *Lycopodio annotini-Sorbetum aucupariae*; 6 – *Listero cordatae-Piceetum abietis*; 7 – *Sphagno capillifolii-Piceetum abietis*.

Division of the diagnostic species into differential and Braun-Blanquetian character species is not applied, because (1) this statistical evaluation is based only on limited dataset, (2) character species (for example for Slovak vegetation) are often traditionally selected subjectively, even in the national monographs, and thus do not rely on statistical determination (for example *Adenostyles alliariae*).

Species taxa names from the Western Carpathian relevés follow checklists of MARHOLD et al. (1998), KUBINSKÁ & JANOVICOVÁ (1998) and PIŠÚT et al. (1998), with exception of the *Soldanella marmarossiensis* agg. (*S. hungarica* auct. slov., VALACHOVIČ et al. 2019); other not included taxa names (marked by †) are applied according to GBIF checklist (GBIF Secretariat 2021). Nomenclatural evaluation of the discussed syntaxa names is regulated according to the 4<sup>th</sup> edition of the Code (THEURILLAT et al. 2021), highlighted are the cited Code Articles ('Art.') and Recommendations ('Rec.'). The names of the classes *Vaccinio-Piceetea* Br.-Bl. in Br.-Bl. et al. 1939 and *Carpino-Fagetea* Jakucs ex Passarge 1968 are hereafter given without author citations.

The used common soil names supplemented by the edition 2006 of the World Reference Base for Soil Resources names are applied according to the reference table in the 'Societas pedologica Slovaca' (2014). The sites of the analysed relevés within the individual associations in Slovakia are given in the Figures 2 and 3. The coordinates of the dataset relevés taken from the CDF were either originally assigned by the present author or partially revised, especially those created for older surveys without pre-existing coordinate data. The maps were created using the Free and Open Source QGIS (QGIS.org 2021), the base layer (terrain) is provided by Geodesy, Cartography and Cadastre Authority of the Slovak Republic (see <https://zbgis.skgeodesy.sk>).

Extended characterization of the discussed associations – their distribution within the Western Carpathians, ecology, dynamics of the stand, notes on nature conservation – is summarized by

Kučera (in red.). In this paper following aspects are mainly discussed: floristical differentiation, syntaxonomical variability as well as important nomenclatural and syntaxonomical problems.

## Results and discussion

### 1. Reflections on the general delimitation of the considered plant communities

Regionally developed intrazonal coniferous orobiomes (i.e. within the nemoral zone) of the main Central European mountain ranges are analogous counterparts of the taiga (zono)biom of the northern Eurasian latitudes. The most frequent and usually the exclusive component of these orobiomes is a *Picea abies* mountain woodland, only the most highest mountain ranges (Alps, Tatra Mountains etc.) possess a (mixed) *Pinus cembra* woodland.

Due to the impacts of pre-/historical land management, general patterns of the distribution of Norway spruce stands in the Western Carpathians have considerably changed. Fully in agreement with ZLATNÍK (1959: 20), I am of the opinion that the key to understand the original [primary] overall composition of forests in Slovakia is a reconstruction of the natural distribution of *Fagus sylvatica* and its proportional participation in the composition of these forests (for details see KUČERA 2022).

Numerous *Picea abies* plant communities were historically syntaxonomically included into the class *Vaccinio-Piceetea*. However, from the scientific (phytocoenological, ecological etc.) point of view as well as in consideration of the nature conservation goals, (A) natural *Picea abies* communities (incl. their anthropogenically degraded forms) should be differentiated from (B) substitute Norway spruce stands which originated by means of (historical) plantations (direct anthropogenic origin) or by spontaneous secondary succession on deforested areas (subanthropogenic origin). However, in both cases these are habitats which would be naturally occupied by natural mixed *Fagus* forests. In other words, this approach means differentiation of (A) *Picea abies* orobiomes (i.e. occurrences of the supramontane altitudinal vegetation zone *Picea* woodland in the respective mountain ranges) as well as extragradal occurrences of natural *Picea abies* woodland from (B) replacement/substitute *Picea* forests of the montane (sensu stricto) altitudinal vegetation zone (cf. KUČERA 2022).

As montane Norway spruce plantations represent more or less anthropogenically influenced stages of original plant communities of the class *Carpino-Fagetea*, they should be classified within that class (cf. HADAČ & SOFRON 1980; and corrections by KUČERA 2012a, chap. 5.27; see also ZLATNÍK 1975: 83–84, 86). This phytocoenological approach represents a syntaxonomical segregation of (A) the *Vaccinio-Piceetea* communities from (B) all substitute *Picea* stands replacing natural woodlands of the class *Carpino-Fagetea*.

In the field, the latter group is most easily recognized by spontaneous secondary succession of *Fagus sylvatica* which would result decades later in a changed tree species composition in favour of *Fagus* (together with *Abies alba*, *Acer* spp. etc.) or – in the higher montane elevations – development of mixed deciduous-coniferous woodlands with *Fagus* keeping an important ecological influence on development of the field layer species composition. However, silvicultural management practices often negatively impact or suppress that processes of the reverse succession. On the contrary, *Vaccinio-Piceetea* woodlands are lacking the signs of *Picea* vs. *Fagus* successional replacement and also other floristical attributes are present, especially the common occurrence

of oreal species (*Adenostyles alliariae*, *Athyrium distentifolium*, *Calamagrostis villosa*, *Homogyne alpina*, *Gentiana asclepiadea* etc.) (see KUČERA 2022).

Several variants of the elevational span of the supramontane vegetation zone were published for the Western Carpathians (see KUČERA 2012a: chapter 3). Apart of their mutual inconsistency, the recent field research supported by old orthophoto records ('Historická ortofotomap Slovenska' s. d. [online]) served for substantial revision of (1) data on the natural altitudinal distribution of (mixed) upper montane *Fagus* woodland in the Western Carpathians as well as (2) theories on the distribution of so-called *Fagus*-free coniferous woodlands in the middle and lower montane altitudes of Slovak basins and mountain ranges (for details see e.g. KUČERA 2012a,b, 2022; KUČERA et al. 2013). In Slovakia, the general lower altitudinal limit of the supramontane zone most probably has not naturally descended below 1350 m a.s.l. at all. In respect of various expositions and mountain ranges, the estimated range is probably within the interval between (1370)1380–1430(1450) m a.s.l.

The extrazonal natural occurrences of Norway spruce communities in lower altitudes are obviously not counted to that range, because the respective communities originated in terrain-induced ecologically extreme habitats inhibiting the development of so-called climax woodland forming the predominating woodland vegetation (cf. also ZLATNÍK 1975: 103–104 and OBERDORFER 1978: 327–328). Such ecologically peculiar Norway spruce communities are altitudinally lying in various elevations of the montane belt occupied by communities of the class *Carpino-Fagetea* (KUČERA 2022). Considering the natural acid Norway spruce woodland types, the most frequent example of such extrazonal communities are phytocoenoses of the association *Listero cordatae-Piceetum* (Samek et al. 1957) Kučera 2023 developed on scree habitats.

A detailed review of Norway spruce woodlands documented in the individual mountain ranges of the Western Carpathians as well as comments to communities incorrectly classified within the class *Vaccinio-Piceetea* was already published (see KUČERA 2012a). A shortened catalogue of records of the plant communities which should not be considered as natural acid Norway spruce communities is given in Table 1. They should be classified as anthropogenic degraded variants of plant communities of the class *Carpino-Fagetea*, either within the order *Luzulo-Fagetalia sylvaticae* Scamoni et Passarge 1959 uniting acid *Fagus* and *Fagus-Abies* woodlands or, eventually, within the group of mesotrophic silicicolous (to semicalcicolous) *Fagus* and *Fagus-Abies* woodlands united into the order *Fagetalia sylvaticae* Tüxen 1931 (cf. BOEUF et al. 2014; KUČERA 2022).

The catalogue given in Table 1 demonstrates that anthropogenic acid Norway spruce phytocoenoses were recorded in rather large number within the Western Carpathians. Probably most of them were used in the specialized statistical surveys on either diagnostic and other significant species (CHYTRÝ et al. 2002b; JAROLÍMEK et al. 2008b; cf. also JAHN 1977) or phytocoenological affinity of a chosen taxon (VALACHOVIČ et al. 2019) – see the very high total number of relevés used in that studies in comparison to the here presented syntaxonomical revision. Therefore, the respective results of those studies are incorrect or misleading when considering the class *Vaccinio-Piceetea*, because they represent a mixture of relevé data of two classes: *Carpino-Fagetea* and *Vaccinio-Piceetea* (KUČERA 2022).

Another example of questionable study result is indication that *Fagus sylvatica* should reach frequency of 42% within the woodland stands classified as the EUNIS habitat 'Temperate mountain

Table 1. Catalogue of the anthropogenic acid (mixed) Norway spruce phytocoenoses incorrectly classified within the class *Vaccinio-Piceetalia*.

Only published studies are listed, for details see KučERA (2007, 2012a). Slovak geomorphological units are given according to KOČÍKÝ & IVANIČ (2011), names of Moravian, Silesian and Polish mountain ranges follow the general use.

## Part 1. Slovakia.

Authors	Geomorphological unit	Originally used unit name	Proportion of degraded <i>Carpino-Fagetum</i> relevés	Remarks
KLIKA (1926)	Veľká Fatra	<i>Piceetum excelsae</i>	All relevés	
KLIKA (1927)	Veľká Fatra	<i>Piceetum (Fagetum) carpaticum myrillotsum</i>	All relevés	
KLIKA (1929)	Krivánska Fatra, Kremnické vrchy	Typ borúvkový. <i>Vaccinium myrtillus-Calamagrostis varia</i>	All relevés	In rel. 32 erroneously <i>Calamagrostis varia</i> (trete <i>C. villosa</i> ).
BRAUN-BLANQUET (1930)	Vysoké Tatry	<i>Piceetum myrillotsum</i>	?	A natural Norway spruce phytocoenosis on bouldery habitat?
ŠOÓ (1930)	Tatranské podhorie, Vysoké Tatry	<i>Piceetum excelsae normale et myrillotsum</i>	Pro parte	Tab. II, col. 5, synoptic table.
SILLINGER (1933)	Kráľovoohorské Tatry	<i>Piceetum excelsae normale silicolum</i>	All relevés	Only synoptic table. Author's original alternative name: <i>Piceeto-Fagetum carpaticum silicolum</i> , type <i>Oxalis-Soldanella</i> .
SILLINGER (1933)	Kráľovoohorské Tatry, Dumbierské Tatry	<i>Piceetum excelsae altherosum silicolum</i>	Pro parte maj.	Only synoptic table.
SILLINGER (1933)	Ďumbierské Tatry, Kráľovoohorské Tatry	<i>Piceetum excelsae myrillotsum siliculum</i>	All relevés	Only synoptic table.
KRAJINA (1933)	Vysoké Tatry, Tatranské podhorie	<i>Piceeto-Chrysanthemetum rotundifoli</i>	All relevés	Community of the class <i>Mulgedio-Aconitea Hadač et Klikta</i> 1944 (cf. KučERA 2023).
KRAJINA (1933)	Tatranské podhorie, Vysoké Tatry	<i>Piceetum abietis acetosellae silicolum</i>	Pro parte	
KRAJINA (1933)	Vysoké Tatry, Tatranské podhorie,	<i>Myrtillero-calamagrostidetum villosae carpaticum piceetosum abietis</i>	Pro parte min.	
KRAJINA (1933)	Tatranské podhorie, Vysoké Tatry	<i>Vaccinetum myrtilli tetricum piceetosum abietis</i>	Pro parte maj.	
MÍKÝŠKA (1934a)	Vtáčnik	<i>Piceetum myrillotsum</i>	Pro parte	Cf. KučERA (2012a).
MÍKÝŠKA (1934b)	Polana	<i>Piceetum altherbosum</i>	The one present relevé	See also Míkýška (1936b).
MÍKÝŠKA (1934b)	Polana	<i>Piceetum myrillotsum, typ Calamagrostis arundinacea</i>	? The one present relevé	See also Míkýška (1936b).
MÍKÝŠKA (1934b)	Polana	<i>Piceetum myrillotsum, typ Vaccinium myrtillus</i>	? The one present relevé	See also Míkýška (1936b).

Authors	Geomorphological unit	Originally used unit name	Proportion of degraded <i>Carpino-Fagetum</i> relevés	Remarks
KLIKA (1936)	Velká Fatra	<i>Piceetum excelsae filicetosum</i>	All relevés	Cf. also KLIKA (1949).
KLIKA (1936)	Velká Fatra	<i>Piceetum excelsae myrriletosum</i>	All relevés	Cf. also KLIKA (1949).
MÍKÝŠKA (1936a)	Vtáčnik	<i>Piceetum excelsae myrriletosum</i>	Pro parte	Cf. KUČERA (2012a).
MÍKÝŠKA (1939)	Polana	<i>Piceetum myrriletosum præfætricum</i>	Both two present relevés	
SVOBODA (1939)	Západné Tatry	<i>Piceetum oxidatetosum</i>	All relevés	
SVOBODA (1939)	Západné Tatry	<i>Piceetum myrriletosum</i>	Pro parte	
SVOBODA (1939)	Západné Tatry	<i>Piceetum altherbosum</i>	Pro parte	
MÁRÁZ (1956)	Lúčanské Večerné hole	<i>Sorbo-Piceetum myrriletosum</i>	Both two present relevés	
GREBENŠČIKOV et al. (1956)	Oravská Magura	Sorbeto-Piceetum [group of forest types]	All relevés	
SAMEK et al. (1957)	Vysoké Tatry	<i>Piceetum myrriletosum/Homogyno-Piceetum</i>	Pro parte	
SAMEK et al. (1957)	Vysoké Tatry	<i>Piceetum normale silicicolum</i>	All relevés	Phytocoenoses in fact influenced by carbonate rocks.
ZAHRADNÍKOVÁ-Rošetzká (1957)	Ďumbierske Tatry	<i>Piceetum excelsae normale silicicolum</i> Sillinger 1933	–	(Without relevés.)
MIAĐOK (1969)	Veľké vrchy	<i>Piceetum excelsae normale silicicolum</i> Sillinger 1933	All relevés	
MIAĐOK (1969)	Veľké vrchy	<i>Piceetum alivetis oxalidetosum acerofætæ silicicolum</i>	All relevés	
HADAČ et al. (1969)	Bielianske Tatry	<i>Dryoptero-Piceetum exceduae Březina et Hadač in Hadač et al. 1969</i>	All relevés	The original relevés represent two different communities (calcicolous: 119, 185, 254 vs siliciculous: 225, 253).
HADAČ et al. (1969)	Bielianske Tatry	<i>Sphagno-Piceetum exeduae Březina et Hadač in Hadač et al. 1969</i>	All relevés	Cf. HADAČ (1987).
HADAČ et al. (1969)	Bielianske Tatry	<i>Avenello-Piceetum exeduae Hadač et al. 1969 ass. prov.</i>	All relevés	Cf. KUČERA (2010a).
ZLATNIK (1970)	Vysoké Tatry	group of forest types Sorbi aucupariae piceeta	Pro parte	
HORÁK (1971)	Západné Tatry	groups of forest types: Piceeta pinea, Piceeta abietina	All relevés	
HORÁK (1971)	Západné Tatry	group of forest types: Piceeta sorbina	Pro parte	
ŠMARDA et al. (1971)	Bielianske Tatry	<i>Sorbo-Piceetum silicicolum</i> Szafer et al. 1927	All relevés	
ŠOMŠÁK (1973)	Volovské vrchy	<i>Vaccinio myrtilli-Piceetum</i> (Szafer et al. 1923) Šoltés 1971 [originally nom. ined.]	All relevés	Vaccinio myrtilli-Piceetum [Šoltés ex] Šomšák 1973 non Šoltés 1976.

Cont. Table 1. Part 1: Slovakia.

Authors	Geomorphological unit	Originally used unit name	Proportion of degraded <i>Carpino-Fagetae</i> relevés	Remarks
MAGIC & MÁJOVSKÝ (1974)	Stoličké vrchy	<i>Chrysanthemo-Piceion</i> Krajina 1933	All relevés	Only synoptic table.
MAGIC & MÁJOVSKÝ (1974)	Stoličké vrchy	<i>Vaccinio-Abetion</i> Oberdorfer 1962	All relevés	Only synoptic table.
MAGIC & MÁJOVSKÝ (1974)	Stoličké vrchy	<i>Eu-Piccenion</i> Oberdorfer 1957	? All relevés	Only synoptic table.
KUBIČEK & JURKO (1975)	Skorušinské vrchy, Západné Tatry	<i>Fago-Piceetum luzuletosum</i> Kubíček et Jurko 1975	All relevés	
KUBIČEK & JURKO (1975)	Skorušinské vrchy, Západné Tatry	<i>Vaccinio myrtilli-Piceetum typicum</i> Šoltés 1971 [originally nom. ined.]	All relevés	<i>Vaccinio myrtilli-Piceetum typicum</i> [Šoltés ex] Kubíček et Jurko 1975 non Šoltés 1976.
KUBIČEK & JURKO (1975)	Západné Tatry	<i>Adenostylo-Piceetum typicum</i> Šoltés 1971 [originally nom. ined.]	Pro parte maj.	<i>Adenostylo-Piceetum typicum</i> [Šoltés ex] Kubíček et Jurko 1975 non Šoltés 1976.
ŠOLTÉS (1976)	Vysoké Tatry, Tatranské podhorie	<i>Adenostylo-Piceetum typicum</i>	?	Only newly published relevé is considered (Šoltés 1976, tab. 1, col. 10).
ŠOLTÉS (1976)	Vysoké Tatry, Tatranské podhorie	<i>Vaccinio myrtilli-Piceetum typicum</i>	Pro parte	Only newly published relevés are considered (Šoltés 1976, tab. 4).
FAJMONOVÁ (1978)	(not specified)	<i>Adenostylo-Piceetum</i> (Sillinger 1933) Šoltés 1976	?	(Without further information on included relevés.)
ŠOMŠÁK et al. (1979)	Popradská kordína	community <i>Luzula pilosa-Picea abies</i>	Both two present relevés	
ŠOMŠÁK et al. (1979)	Vysoké Tatry	community <i>Calamagrostis villosa-Picea abies</i> ( <i>Vacc myrtilli-Piceetum</i> Šoltés 1976)	Both two present relevés	
FAJMONOVÁ (1978)	Kráľovohorské Tatry	<i>Vaccinio myrtilli-Piceetum</i> (Szafer et al. 1923) Šoltés 1971 [originally nom. ined.]	All relevés	Only synoptic table.
FAJMONOVÁ (1980)	(higher number of units)	<i>Vaccinio myrtilli-Piceetum</i> (Szafer et al. 1923) Šoltés 1971 [originally nom. ined.]	Pro parte	Only synoptic table.
NÍČ (1981)	Oravské Beskydy	group of forest types <i>Sorbo-Piceetum</i>	Pro parte maj.	
ŠOMŠÁK et al. (1981)	Vysoké Tatry	<i>Adenostylo-Piceetum</i> (Sillinger 1933) Šomšák 1976	Rel. 1	(Potential natural vegetation with <i>Acer pseudoplatanus</i> , <i>Abies alba</i> , <i>Fagus sylvatica</i> , <i>Picea abies</i> in the canopy.)
MAJZLANOVÁ (1982)	Skorušinské vrchy	<i>Vaccinio myrtilli-Piceetum</i> (Szafer et al. 1923) Šoltés 1976	All relevés	Cf. Majzlanová (1993).

Authors	Geomorphological unit	Originally used unit name	Proportion of degraded <i>Carpino-Fagetae</i> relevés	Remarks
ŠOMŠÁK (1983)	Oravská Magura	<i>Athyrio alpetris-Piceetum</i> F.K. Hartmann 1959 [originally nom. nud.]	All relevés	
UNAR et al. (1984)	Západné Tatry	<i>Piceetum excelsae myrtillaeum</i> Szafer et al. 1923	All relevés	
LEPŠ et al. (1985)	Ďumbierske Tatry	<i>Vaccinio-Piceion</i> Br.-Bl. in Br.-Bl. et al. 1939	Pro parte maj.	... a mosaic of <i>Calamagrostio villosae-Piceetum</i> (Tx. 1937) Hartmann 1953 and <i>Vaccino myrtilli-Piceetum</i> (Szafer et al. 1923) Šoltés 1976.
MĽADOK (1988)	Veporské vrchy	<i>Abieto Piceetum</i> (Szafer et al. 1923) Samek et al. 1957	All relevés	
MĽADOK (1988)	Veporské vrchy	<i>Vaccinio myrtilli-Piceetum typicum</i> Šoltés 1976	Pro parte maj.	
MĽADOK (1988)	Veporské vrchy	<i>Oxalido-Piceetum</i> Břízna et Hadač et al. 1969	All relevés	
MĽADOK (1988)	Veporské vrchy	<i>Dryoptero-Piceetum excelsae</i> Břízina et Hadač et al. 1969	All relevés	
MĽADOK (1988)	Veporské vrchy	<i>Athyrio alpetris-Piceetum</i> Hartmann et Jahn 1967	All relevés	
KUBÍČEK et al. (1989)	Moravsko-slezské Beskydy	<i>Vaccinio myrtilli-Piceetum</i> Szafer et al. 1923) Šoltés 1976	All relevés	
VOŠKO et al. (1990)	Vysoké Tatry (? mostly), Tatranské podhorie	groups of forest types: <i>Piceeta sorbina</i> , <i>Piceeta pineolaricina</i> , <i>Abieti-Piceeta laricis</i>	All relevés	
KUBÍČEK et al. (1992)	Vysoké Tatry	<i>Vaccinio myrtilli-Piceetum</i> (Szafer et al. 1923) Šoltés 1976	? Rel. 3.	
KUBÍČEK et al. (1992)	Tatranské podhorie	<i>Chrysanthemo rotundifolii-Piceetum</i> Krajina 1933	Rel. 6.	
KUBÍČEK & ŠOMŠÁK (1993)	Tatranské podhorie Vysoké Tatry	Higher number of units	? All relevés.	(Without published relevés.)
ŠOMŠÁK et al. (1993)	Tatranské podhorie	<i>Chrysanthemo rotundifolii-Piceetum</i> Krajina 1933	–	
ČERNUŠÁKOVÁ (1994)	Západné Tatry	<i>Calamagrostio villosae-Piceetum</i> (Tx. 1937) Hartmann 1953	Pro parte	
ČERNUŠÁKOVÁ (1994)	Západné Tatry	<i>Athyrio alpestre-Piceetum</i> (Hartmann 1953) Hartmann et Jahn 1967)	Pro parte	
MĽADOK (1995)	Ďumbierske Tatry	<i>Vaccinio myrtilli-Piceetum typicum</i> Šoltés 1976	Pro parte min.	
MĽADOK (1995)	Ďumbierske Tatry	<i>Oxalido-Piceetum excelse</i> (Krajina 1933) Břízina et Hadač et al. 1969	Pro parte	
ŠKOLEK (1995a)	Ďumbierske Tatry	<i>Vaccinio myrtilli-Piceetum</i> (Szafer et al. 1923) Šoltés 1976	? All relevés	Only synoptic table.

Cont. Table 1. Part 1: Slovakia.

P. KUČERA

Authors	Geomorphological unit	Originally used unit name	Proportion of degraded <i>Carpino-Fagetum</i>	Remarks
ŠKOLEK (1995b)	Ďumbierske Tatry	<i>Oxalido-Piceetum excelsae</i> Březina et Hadač in Hadač et al. 1969	The one present relevé	
ŠKOLEK (1995b)	Ďumbierske Tatry	<i>Vaccinio myrtilli-Piceetum</i> (Szafer et al. 1923) Šoltés 1976	The one present relevé	
KUKLA et al. (1995)	Poľana	<i>Vaccinio myrtilli-Piceetum</i> (Szafer et al. 1923) Šoltés 1976	All relevés	
KUKLA et al. (1995)	Poľana	<i>Calamagrostio villosae-Piceetum</i> (R. Tx. 1937) Hartmann 1953	All relevés	
KONTRIŠ et al. (1997)	Poľana	All mentioned units.	All relevés	Each syntaxon represented with only one relevé. (Without published relevé.)
ŠKOLEK (2003)	Ďumbierske Tatry	Higher number of units	Pro parte	
KANKA (2008)	Belianske Tatry	<i>Vaccinio myrtilli-Piceetum typicum</i> Šoltés 1976	Pro parte maj.	
KANKA (2008)	Belianske Tatry	<i>Sphagno acutifolii-Piceetum</i> (Březina et Hadač in Hadač et al. 1969) Hadač 1987	All relevés	
KANKA (2008)	Belianske Tatry	<i>Athyrio alpestris-Piceetum</i> Hartmann 1959	Rel. 1, 2	(Rel. 3 & 4 are calcicolous phytocoenoses.)
KANKA (2008)	Belianske Tatry	<i>Dryopterido-Piceetum excelsae</i> Březina et Hadač in Hadač et al. 1969	? Rel. 5	The rest of relevés belong to calcicolous secondary communities, the influence of carbonate rocks on the phytocoenosis of the rel. 5 seems to be considerably small.
KRAJCI (2008)	Kráľovooholské Tatry	<i>Vaccinio myrtilli-Piceetum</i> (Szafer et al. 1923) Šoltés 1976	Pro parte maj.	Cf. also KRAJCI & BARANČOK (2009).
KRAJCI (2008)	Kráľovooholské Tatry	<i>Athyrio alpestris-Piceetum</i> Hartmann 1959	Pro parte	Cf. also KRAJCI & BARANČOK (2009).
KRAJCI (2008)	Kráľovooholské Tatry	<i>Adenostylo-Piceetum</i> Hartmann 1953	All relevés	Cf. also KRAJCI & BARANČOK (2009).
KRAJCI & BARANČOK (2009)	Kráľovooholské Tatry	<i>Sphagno acutifolii-Piceetum</i> (Březina et Hadač in Hadač et al. 1969) Hadač 1987	One relevé only	
JANČOVICOVÁ et al. (2011)	Veporské vrchy	<i>Vaccinio myrtilli-Piceetum</i> Šoltés 1976	Pro parte maj.	
VALACHOVIC et al. (2019)		<i>Piceion excelsae</i>	Pro parte	Authors evaluated only relevés with presence of genus <i>Soldanella</i> .

Part 2. Selected examples from the Western Carpathian mountain ranges in Moravia (M), Silesia (S) and Poland (P).

Authors	Geomorphological unit	Originally used unit name	Proportion of degraded <i>Carpinno-Fagetea</i> relevés	Remarks
SZAFER et al. (1923)	Tatry Zachodnie (P)	<i>Piceetum myrtillotum</i>	Pro parte	<i>Piceetum myrtillotum</i> sensu Szafer et al. 1923 [non Beger 1922].
PAWŁOWSKI (1925)	Beskid Sadecki (P)	<i>Piceetum excelsae filicetorum</i>	The one present relevé	
PAWŁOWSKI (1925)	Beskid Sadecki (P)	<i>Piceetum vacciniosum</i>	The one present relevé	
SZAFER et al. (1927a)	Tatry Zachodnie (P)	<i>Piceetum myrtillotum</i>	All relevés	
PAWŁOWSKI et al. (1928)	Tatry Wysokie (P)	<i>Piceetum excelsae normale</i>	Both two present relevés	
WALAS (1933)	Beskid Żywiecki (P)	<i>Piceetum excelsae</i>	Pro parte maj. (? all relevés)	
KAWECKI (1939)	Beskid Żywiecki (P)	<i>Piceetum excelsae</i>	All relevés	
MEDWECKA-KORNAŚ (1955)	Gorce (P)	<i>Piceetum taricum abietosum</i>	All relevés	
MEDWECKA-KORNAŚ (1955)	Gorce (P)	<i>Piceetum taricum subnormale</i>	All relevés	
MYCZKOWSKI & GRABSKI (1962)	Beskid Sadecki (P)	<i>Vaccinio-Piceion</i>	All relevés	
PANCER-KOTTEJOWA (1965)	Pogórze Gubalskie (P)	<i>Piceetum taricum abietosum</i>	All relevés	
PANCER-KOTTEJOWA (1965)	Pogórze Gubalskie (P)	<i>Piceetum taricum subnormale</i>	All relevés	
STUCHLIK(1968)	Gorce (P)	<i>Piceetum montanum</i> Szafer et al. = <i>Piceetum (taricum) abietosum</i> Medwecka-Kornaś 1955	All relevés	
STUCHLIK(1968)	Gorce (P)	<i>Piceetum excelsae carpaticum</i> Szafer et al. 1923 = <i>Piceetum (taricum) subnormale</i> Medwecka-Kornaś 1955	All relevés	
MATUZKIEWICZ (1977)	Beskid Żywiecki (P)	<i>Plagiothecio-Piceetum taricum</i> (Szafer et al. 1923 p.p.) J. Matuszkiewicz 1977	Pro parte maj. (? all relevés)	(As given within Tab. 7.)

Cont. Table 1. Part 2: Moravia (M), Silesia (S) and Poland (P).

Authors	Geomorphological unit	Originally used unit name	Proportion of degraded <i>Carpino-Fagetum</i> relevés	Remarks
MATUZKIEWICZ (1977)	(higher number of units) (P)	<i>Abieti-Piceetum montanum</i> W. Matuszkiewicz 1967	—	Entire unit.
MATUZKIEWICZ (1977)	(higher number of units) (P)	<i>Gallio rotundifoli-Piceetum carpaticum</i> J. Matuszkiewicz 1977	—	Entire unit.
SEDLÁČKOVÁ (1978)	Moravsko-slezské Beskydy (M)	<i>Vaccinio-Piceetalia</i>	All relevés	
SEDLÁČKOVÁ (1978)	Moravsko-slezské Beskydy (M)	<i>Athyrio-Piceetalia</i> ( <i>Athyrio alpestris-Piceetum</i> Hartmann 1959)	All relevés	
CELIŃSKI & WOJTERSKI (1978)	Beskid Żywiecki (P)	<i>Piceetum excelsae carpaticum</i> (Szafer et al. 1923) Br.-Bl. et al. 1939 [three subunits]	Pro parte maj. (? all relevés)	
CELIŃSKI & WOJTERSKI (1978)	Beskid Żywiecki (P)	<i>Abieti-Piceetum montanum</i> Szafer et al. 1923	All relevés	In two relevés <i>Fagus</i> co-dominates. Cf. also , <i>Galio-Abietetum</i> Wraber (1955) 1959 <sup>c</sup> .
FAJMONOVÁ (1980)	Moravsko-slezské Beskydy (M, S)	<i>Vaccinio myrtilli-Piceetum</i> (Szafer et al. 1923) Šoltés 1971 [originally nom. ined.]	All relevés	Only synoptic table from multiple mountain ranges.
JIRÁSEK (1996)	Moravsko-slezské Beskydy (M)	<i>Calamagrostio villosae-Piceetum typicum</i> var. <i>calamagrostiosum arundinaceae</i> Jirásek 1996	The one present relevé from the MS Beskyds	Entire unit.
JIRÁSEK (1996)	Moravsko-slezské Beskydy (M, S)	<i>Calamagrostio villosae-Piceetum fagerosum</i> Jirásek 1996	—	Entire unit. Without recorded relevé from the considered region.
JIRÁSEK (1996)	Moravsko-slezské Beskydy (M, S)	<i>Athyrio alpestris-Piceetum typicum</i> var. <i>calamagrostiosum arundinaceae</i> Jirásek 1996	Rels. 4, 5	Entire unit. Partly also var. <i>typicum</i> .
JIRÁSEK (1996)	Moravsko-slezské Beskydy (M, S)	<i>Athyrio alpestris-Piceetum athyrietorum filicis-fenniae</i> Hartmann et Jahn 1967	—	Without recorded relevé from the considered region. According to the author probably distributed also in the Moravian-Silesian Beskyds.
KASPROWICZ (1996)	Beskid Żywiecki (P)	<i>Abieti-Piceetum montanum</i> (Szafer et al. 1923) Celiński et Wojsierski 1961 n. n.	All relevés	In some relevés <i>Fagus</i> predominates. Cf. also , <i>Galio-Abietetum</i> Wraber (1955) 1959 <sup>c</sup> .
KASPROWICZ (1996)	Beskid Żywiecki (P)	<i>Plagiothecio-Piceetum</i> (Szafer et al. 1923) Br.-Bl. et al. 1939 em. J. Matuszkiewicz 1978	Pro parte	Minor part of relevés belongs to the order <i>Sphagneto palustris-Piceetalia</i> P. Kučera 2019 (cf. tab. 31).

*Picea* forest' (see CHYTRÝ et al. 2020). In the same way as exemplified above, this controversial outcome resulted from calculations performed on partial *Picea*-forest dataset consisting of mixture of (1) true (natural or close to natural) *Picea abies* woodland samples (*Vaccinio-Piceetea*) + other samples of *Vaccinio-Piceetea* communities and (2) substitutionary (mixed) *P. abies* forest samples replacing the original mixed *Fagus sylvatica* woodlands (*Carpino-Fagetea*) with spontaneous reverse secondary succession of *F. sylvatica*. Admixture of this second group, incorrectly classified within 'Temperate mountain *Picea* forest', causes the inappropriate high frequency value of *Fagus* calculated for the respective EUNIS habitat. The recently published map of vegetation alliances in Europe (PREISLEROVÁ et al. 2022) is affected by the same error with very high probability.

Moreover, another incorrect approach is the application of the term 'mountain taiga' for Central European Norway spruce forests of higher mountain-ranges (see CHYTRÝ 2012), especially in the case if in this way are labelled substitute non-natural forest stands replacing the various former *Carpino-Fagetea* woodlands (KUČERA 2012a; e.g. within the Moravian-Silesian Beskids). The mentioned term should be applied precisely only to mountain woodlands in the region of Euro-Siberian taiga, i.e. to a real mountain taiga – for example in the Northern Urals.

## 2. Associations of acid Norway spruce woodland in Slovakia

Seven basic natural acid Norway spruce plant communities are differentiated in this syntaxonomical revision. The most species-poor phytocoenoses are included within the association *Lophozio-Piceetum* which is typical of so-called mittelgebirge mountain ranges (cf. KUČERA 2022) and represents there the most widespread natural *Picea abies* community; however, it could be also found in the Tatras and the Low Tatras. The stands of the association *Athyrio distentifolii-Piceetum* are developed on special more humid habitats, where they alternate with the previous community. The recently distinguished association *Sphagno capillifolii-Piceetum* represents a marginal community within the group of natural acid Norway spruce woodland types – it comprises communities in spatial contact with supramontane bog communities and other related communities.

During this syntaxonomical revision, four new distinctive habitat-specific and phytocoenologically independent plant communities were distinguished. The associations *Solidagini virgaureae-Piceetum* (ecological counterpart of *Athyrio-Piceetum*) and *Parido quadrifoliae-Piceetum* (on relatively rare trophically intermediate habitats) are exclusively bound to hochgebirge mountain ranges (mostly the Tatra mountains). In special scree habitats phytocoenoses of the association *Listero cordatae-Piceetum* are found. *Lycopodio annotini-Sorbetum aucupariae* comprises a special *Sorbus aucuparia* dominated and a floristically rich community developed on windthrow sites.

### 2.1. *Lophozio-Piceetum abietis* Volk in Br.-Bl. et al. 1939 nom. corr.

Nomenclatural type: HARTMANN & JAHN (1967), tab. 2, rel. 10, neotypus hoc loco.

Original name: *Lophozieto-Piceetum* Volk 1939 mss. (BRAUN-BLANQUET et al. 1939: 30), i.e.

*Lophozio-Piceetum excelsae* Volk in Braun-Blanquet et al. 1939 nom. incept. (Rec. 10C, Art. 41b, Art. 44)

Syntax. syn.: *Piceetum abietis oxalidetosum acetosellae silicicolum* Krajina 1933 nom. inval. (Art. 3e) p.p., *Piceetum excelsae* Tx. 1937 nom. illeg. (Art. 31) (p.p.) ≡ *Piceetum hercynicum* Tx. in Br.-Bl. et al. 1939 nom.

illeg. (Art. 34a) (p.p.) ≡ *Plagiothecio-Piceetum hercynicum* (Tx. in Br.-Bl. et al. 1939) J. Matuszkiewicz 1977 nom. illeg. (Art. 34a) (p.p.),

Table 2. Statistical comparison of associations of the alliance *Piceion abietis* Pawłowski ex Pawłowski et al. 1928 in Slovakia with values of constancy (%) and fidelity ( $\phi \times 100 \geq 25$ ) in the exponent  
Field and ground layer species represented in only one column are omitted.

Group 1 – *Lophozio-Piceetum abietis* Volk in Br.-Bl. et al. 1939 nom. corr.

Group 2 – *Athyrio distentifolii-Piceetum abietis* Hartmann ex Hartmann et Jahn 1967 nom. corr.

Group 3 – *Solidagini virgaureae-Piceetum abietis* P. Kučera in P. Kučera et al. 2023

Group 4 – *Parido quadrifoliae-Piceetum abietis* P. Kučera in P. Kučera et al. 2023

Group 5 – *Lycopodio annotini-Sorbetum aucupariae* P. Kučera 2023

Group 6 – *Listero cordatae-Piceetum abietis* (Samek et al. 1957) P. Kučera 2023

Group 7 – *Sphagno capillifolii-Piceetum abietis* Zukrigl 1973 nom. corr.

The quantity of asterisks in the second column expresses the highest state of conventional levels of the statistical significance (0.05, 0.01 and 0.001, Fisher's exact test) for the particular species. In the case of differential species for multiple units such indication could have alternative states.

Group No.	1	2	3	4	5	6	7
No. of relevés	40	16	21	11	8	7	6
<b>Tree and shrub species</b>							
<b>Canopy (E<sub>3</sub>)</b>							
<i>Picea abies</i>	<b>100</b> –	<b>100</b> –	<b>100</b> –	<b>100</b> –	<b>75</b> –	<b>100</b> –	<b>100</b> –
<i>Sorbus aucuparia</i>	***	20 –	31 –	5 –	9 –	<b>100</b> <sup>58.9</sup>	29 –
<i>Larix decidua</i>	*	5 –	6 –	–	27 <sup>31.4</sup>	12 –	–
<i>Betula carpatica</i>	***	–	–	–	–	38 <sup>58.3</sup>	–
<i>Salix caprea</i>	–	–	–	–	–	12 –	–
<i>Salix silesiaca</i>	–	–	–	–	–	–	14 –
<b>Understorey</b>							
E <sub>2</sub>							
<i>Picea abies</i>	35 –	25 –	10 –	<b>64</b> <sup>24.8</sup>	<b>62</b> –	14 –	33 –
<i>Sorbus aucuparia</i>	8 –	25 –	5 –	36 <sup>21.5</sup>	12 –	14 –	17 –
<i>Pinus mugo</i>	10 –	6 –	–	18 –	–	14 –	33 –
<i>Ribes petraeum</i>	2 –	–	–	–	–	–	–
<i>Salix silesiaca</i>	2 –	–	–	–	–	–	–
<i>Sambucus racemosa</i>	–	6 –	–	–	–	–	–
<i>Salix caprea</i>	–	–	–	9 –	–	–	–
<i>Lonicera nigra</i>	–	–	–	–	12 –	–	–
<i>Abies alba</i>	–	–	–	–	12 –	–	–
<i>Fagus sylvatica</i>	–	–	–	–	–	–	17 –
E <sub>1</sub>							
<i>Sorbus aucuparia</i>							
<i>Picea abies</i>	<b>80</b> –	<b>88</b> –	<b>100</b> <sup>15.4</sup>	<b>91</b> –	<b>88</b> –	<b>100</b> –	<b>67</b> –
<i>Lonicera nigra</i>	***	2 –	19 –	10 –	18 –	<b>75</b> <sup>61.3</sup>	–
<i>Abies alba</i>	*	2 –	–	–	–	25 <sup>23.6</sup>	–
<i>Pinus cembra</i>	2 –	6 –	–	18 –	–	14 –	–
<i>Fagus sylvatica</i>	5 –	6 –	–	–	–	–	–
<i>Ribes petraeum</i>	–	12 –	5 –	–	–	–	–
<i>Larix decidua</i>	2 –	–	–	9 –	–	–	–
<i>Salix</i> sp.	–	6 –	–	–	–	–	17 –
<i>Pinus mugo</i>	**	–	–	–	–	–	<b>33</b> <sup>54.8</sup>
<i>Sambucus racemosa</i>	–	–	5 –	–	–	–	–
<i>Salix silesiaca</i>	–	–	–	–	12 –	–	–

Group No.	1	2	3	4	5	6	7
<b>Differential field layer species (E<sub>1</sub>)</b>							
<i>Trientalis europaea</i>	*	10 <sup>29.5</sup>	—	—	—	—	—
<i>Acetosa arifolia</i>	***	—	56 <sup>56.0</sup>	14—	—	12—	—
<i>Soldanella marmarossiensis</i> agg.	***	18—	50 <sup>44.3</sup>	—	—	25—	—
<i>Milium effusum</i>	*	—	31 <sup>28.1</sup>	29 <sup>24.5</sup>	—	12—	—
<i>Solidago virgaurea</i>	***	5—	6—	76 <sup>66.1</sup>	—	12—	14—
<i>Adenostyles alliariae</i>	***	15—	62—	100 <sup>48.8</sup>	18—	50—	43—
<i>Hieracium murorum</i>	***	2—	—	24 <sup>43.0</sup>	—	—	—
<i>Rubus idaeus</i>	***	35—	69—	81 <sup>31.3</sup>	27—	75—	14—
<i>Melampyrum sylvaticum</i>	***	5—	—	—	55 <sup>59.5</sup>	12—	—
<i>Paris quadrifolia</i>	***	—	—	—	45 <sup>55.1</sup>	12—	—
<i>Epilobium montanum</i>	**	2—	—	—	27 <sup>46.6</sup>	—	—
<i>Blechnum spicant</i>	**	—	6—	—	27 <sup>43.0</sup>	—	—
<i>Chaerophyllum hirsutum</i>	**	—	—	—	18 <sup>40.0</sup>	—	—
<i>Galeobdolon montanum</i>	**	—	—	—	18 <sup>40.0</sup>	—	—
<i>Luzula pilosa</i>	*	—	6—	—	18 <sup>32.7</sup>	—	—
<i>Gymnocarpium dryopteris</i>	***	5—	19—	—	—	75 <sup>55.7</sup>	43 <sup>23.0</sup>
<i>Hylotelephium argutum</i>	**	—	—	5—	—	38 <sup>53.9</sup>	—
<i>Dryopteris filix-mas</i>	**	2—	6—	—	—	38 <sup>50.8</sup>	—
<i>Doronicum austriacum</i>	**	5—	19—	19—	—	50 <sup>44.2</sup>	—
<i>Prenanthes purpurea</i>	**	15—	31—	52 <sup>13.5</sup>	55—	88 <sup>43.3</sup>	14—
<i>Ranunculus platanifolius</i>	*	—	—	10—	—	25 <sup>37.8</sup>	—
<i>Listera cordata</i>	***	—	6—	—	—	71 <sup>78.4</sup>	—
<i>Huperzia selago</i>	**	5—	12—	—	—	43 <sup>49.8</sup>	—
<i>Veratrum album</i> ssp. <i>lobelianum</i>	**	12—	50 <sup>24.2</sup>	—	—	38—	71 <sup>44.6</sup>
<i>Carex canescens</i>	***	2—	—	—	—	—	83 <sup>88.5</sup>
<i>Nardus stricta</i>	***	2—	6—	—	—	—	83 <sup>84.8</sup>
<i>Juncus filiformis</i>	***	—	—	—	—	—	67 <sup>79.5</sup>
<i>Eriophorum vaginatum</i>	***	—	—	—	—	—	50 <sup>67.9</sup>
<i>Carex echinata</i>	***	—	—	—	—	—	50 <sup>67.9</sup>
<i>Carex nigra</i>	***	—	—	—	—	—	50 <sup>67.9</sup>
<b>Differential species for two or more associations</b>							
<i>Stellaria nemorum</i>	***	5—	62 <sup>45.8</sup>	—	64 <sup>47.0</sup>	—	—
<i>Luzula luzuloides</i>	***	8—	56—	95 <sup>43.1</sup>	100 <sup>47.1</sup>	25—	—
<i>Calamagrostis arundinacea</i>	***/*	12—	19—	38—	100 <sup>58.0</sup>	62 <sup>25.5</sup>	—
<i>Athyrium filix-femina</i>	***/**	5—	19—	48 <sup>11.8</sup>	91 <sup>49.2</sup>	75 <sup>35.4</sup>	—
<i>Lycopodium annotinum</i>	***/*	10—	—	—	—	50 <sup>25.5</sup>	71 <sup>46.1</sup>
<i>Athyrium distentifolium</i>	**/*	38—	75 <sup>22.2</sup>	5—	9—	25—	100 <sup>42.7</sup>
<i>Senecio nemorensis</i> agg.	***/**	8—	50—	100 <sup>41.0</sup>	91 <sup>33.6</sup>	100 <sup>41.0</sup>	—
<b>Other field layer species (E<sub>1</sub>)</b>							
<i>Vaccinium myrtillus</i>		100—	94—	100—	100—	88—	100—
<i>Homogyne alpina</i>		92—	88—	90—	91—	100—	100—
<i>Dryopteris carthusiana</i> agg.		90—	94—	81—	82—	100—	100—
<i>Oxalis acetosella</i>		95—	100—	90—	91—	75—	100—
<i>Avenella flexuosa</i>		90—	56—	100 <sup>19.0</sup>	45—	100—	100—
<i>Calamagrostis villosa</i>		85—	81—	62—	91—	62—	86—

Group No.	1	2	3	4	5	6	7
<i>Luzula sylvatica</i> ssp. <i>sylvatica</i>	72-	81-	90-	82-	75-	71-	33-
<i>Gentiana asclepiadea</i>	38-	44-	71 <sup>24.1</sup>	9-	62-	71-	-
<i>Vaccinium vitis-idaea</i>	45-	6-	19-	73 <sup>24.4</sup>	38-	71-	50-
<i>Cicerbita alpina</i>	2-	25-	29-	18-	38-	-	-
<i>Polygonatum verticillatum</i>	2-	19-	10-	-	25-	-	-
<i>Maianthemum bifolium</i>	5-	12-	-	-	-	-	-
<i>Streptopus amplexifolius</i>	2-	12-	-	-	12-	-	-
<i>Epilobium angustifolium</i>	-	12-	5-	-	12-	-	-
<i>Ligusticum mutellina</i>	-	12-	5-	-	-	14-	-
<i>Phegopteris connectilis</i>	-	6-	-	9-	12-	14-	-
<i>Luzula alpinopilosa</i>	2-	6-	-	-	-	14-	-
<i>Hieracium lachenalii</i>	2-	6-	5-	-	-	-	-
<i>Valeriana tripteris</i>	-	6-	-	-	12-	14-	-
<i>Luzula luzulina</i>	2-	6-	-	-	-	-	-
<i>Deschampsia cespitosa</i>	-	6-	-	-	-	-	17-
<i>Mycelis muralis</i>	2-	-	-	-	-	-	-
<i>Bistorta major</i>	2-	-	-	-	-	-	-
<i>Hypericum maculatum</i>	-	6-	-	-	-	-	-
<i>Delphinium elatum</i>	-	6-	-	-	-	-	-
<i>Rumex obtusifolius</i>	-	6-	-	-	-	-	-
<i>Oreogenum montanum</i>	-	6-	-	-	-	-	-
<i>Poa chaixii</i>	-	-	-	9-	-	-	-
<i>Hieracium laevigatum</i>	-	-	-	9-	-	-	-
<i>Veronica officinalis</i>	-	-	-	9-	-	-	-
<i>Campanula serrata</i>	-	-	-	9-	-	-	-
<i>Soldanella carpatica</i>	-	-	-	9-	-	-	-
<i>Petasites albus</i>	-	-	-	9-	-	-	-
<i>Agrostis capillaris</i>	-	-	-	9-	-	-	-
<i>Rubus saxatilis</i>	-	-	-	9-	-	-	-
<i>Urtica dioica</i>	-	-	-	-	12-	-	-
<i>Moneses uniflora</i>	-	-	-	-	12-	-	-
<i>Linnaea borealis</i>	-	-	-	-	-	14-	-
<i>Gentiana punctata</i>	-	-	-	-	-	14-	-
<i>Alchemilla</i> sp. div.	-	-	-	-	-	-	17-
<i>Ranunculus acris</i>	-	-	-	-	-	-	17-
<i>Carex pauciflora</i>	-	-	-	-	-	-	17-
<i>Equisetum sylvaticum</i>	-	-	-	-	-	-	17-
<i>Rumex alpinus</i>	-	-	-	-	-	-	17-
<i>Taraxacum</i> sect. <i>Ruderalia</i>	-	-	-	-	-	-	17-
Differential ground layer species (E <sub>0</sub> )							
<i>Plagiothecium curvifolium</i>	***	42-	44-	81 <sup>42.4</sup>	9-	-	50-
<i>Chiloscyphus pallescens</i>	*	2-	-	14 <sup>31.7</sup>	-	-	-
<i>Plagiochila poreloides</i>	***	2-	12-	-	55 <sup>60.9</sup>	-	-
<i>Plagiomnium undulatum</i>	***	-	-	-	36 <sup>57.3</sup>	+	-
<i>Sphagnum girgensohnii</i>	**	15-	6-	-	55 <sup>32.4</sup>	12-	14-
<i>Sphenolobus minutus</i>	***	-	-	-	50 <sup>67.9</sup>	-	-
<i>Lophozia</i> cf. <i>incisa</i>	***	8-	6-	-	62 <sup>67.6</sup>	-	-

Group No.		1	2	3	4	5	6	7
<i>Plagiothecium denticulatum</i>	***	10-	-	-	-	<b>50</b> <sup>60.4</sup>	-	-
<i>Tortella tortuosa</i>	**	2-	-	-	-	38 <sup>55.9</sup>	-	-
<i>Tetraphis pellucida</i>	***	5-	6-	-	-	<b>50</b> <sup>51.6</sup>	14-	-
<i>Blepharostoma trichophyllum</i>	**	12-	12-	-	-	<b>50</b> <sup>45.6</sup>	14-	-
<i>Mnium sp.</i>	*	2-	-	-	-	25 <sup>44.3</sup>	-	-
<i>Bazzania trilobata</i>	***	-	-	-	-	43 <sup>62.6</sup>	-	-
<i>Calypogeia azurea</i>	***	8-	-	-	-	71 <sup>61.6</sup>	33-	-
<i>Cladonia sp.</i>	***	-	6-	-	-	43 <sup>57.3</sup>	-	-
<i>Pleurozium schreberi</i>	***	25-	38-	5-	9-	50-	100 <sup>53.2</sup>	33-
<i>Barbilophozia lycopodioides</i>	***	2-	12-	5-	-	-	57 <sup>52.5</sup>	17-
<i>Sphagnum recurvum</i> agg.	**	-	-	-	-	-	29 <sup>50.5</sup>	-
<i>Rhytidadelphus squarrosus</i>	*	8-	19-	-	-	-	43 <sup>45.1</sup>	-
<i>Schistidium apocarpum</i>	*	-	6-	5-	-	-	29 <sup>40.5</sup>	-
<i>Plagiothecium undulatum</i>	**	18-	6-	-	9-	25-	57 <sup>40.1</sup>	17-
<i>Plagiothecium laetum</i>	*	2-	12-	-	-	-	29 <sup>29.1</sup>	17-
<i>Polytrichum commune</i>	***	12-	12-	-	-	25-	-	<b>83</b> <sup>66.8</sup>
<i>Barbilophozia floerkei</i>	**	-	-	-	-	-	-	33 <sup>54.8</sup>
<i>Sphagnum rubellum</i>	**	-	-	-	-	-	-	33 <sup>54.8</sup>
<i>Pohlia nutans</i>	**	-	6-	-	-	-	-	33 <sup>48.9</sup>
<i>Lophocolea heterophylla</i>	**	-	-	-	9-	-	-	33 <sup>46.7</sup>
<i>Dicranum montanum</i>	**	5-	19-	-	18-	-	-	<b>50</b> <sup>44.6</sup>
Differential species for two associations								
<i>Hylocomium splendens</i>	***	18-	19-	-	27-	<b>88</b> <sup>41.4</sup>	<b>100</b> <sup>51.9</sup>	17-
<i>Rhytidadelphus triquetrus</i>	***/**	8-	6-	-	9-	<b>62</b> <sup>35.7</sup>	71 <sup>44.1</sup>	17-
<i>Plagiochila asplenoides</i>	*	-	-	-	-	25 <sup>26.6</sup>	29 <sup>32.1</sup>	-
<i>Sphagnum capillifolium</i>	***	10-	6-	-	-	-	<b>86</b> <sup>54.8</sup>	83 <sup>52.6</sup>
Other ground layer species (E <sub>0</sub> )								
<i>Dicranum scoparium</i>		<b>85</b> -	<b>50</b> -	<b>76</b> -	<b>82</b> -	<b>100</b> -	<b>100</b> -	<b>100</b> -
<i>Polytrichum formosum</i>		<b>75</b> -	<b>69</b> -	<b>67</b> -	<b>73</b> -	<b>88</b> -	<b>100</b> -	<b>83</b> -
<i>Lepidozia reptans</i>		18-	19-	5-	-	12-	29-	-
<i>Calypogeia integrifistula</i>		18-	6-	5-	-	25-	-	33-
<i>Plagiomnium affine</i>		12-	19-	10-	18-	12-	-	-
<i>Dicranella heteromalla</i>		8-	6-	-	-	-	14-	17-
<i>Brachythecium starkei</i>		8-	-	-	-	12-	-	17-
<i>Sphagnum quinquefarium</i>		5-	6-	-	-	12-	-	-
<i>Rhizomnium punctatum</i>		2-	12-	-	-	12-	-	-
<i>Brachythecium velutinum</i>		2-	-	-	9-	-	-	17-
<i>Cetraria islandica</i>		2-	6-	-	-	-	14-	-
<i>Plagiothecium succulentum</i>		5-	6-	-	-	-	-	-
<i>Brachythecium reflexum</i>		5-	-	-	-	12-	-	-
<i>Calypogeia muelleriana</i>		5-	-	-	-	-	-	17-
<i>Rhytidadelphus loreus</i>		-	12-	-	-	12-	-	-
<i>Chiloscyphus polyanthos</i>		5-	-	-	-	-	-	-
<i>Plagiothecium sp.</i>		2-	-	-	-	12-	-	-
<i>Entodon schleicheri</i>		5-	-	-	-	-	-	-
<i>Cladonia furcata</i>		5-	-	-	-	-	-	-

Group No.	1	2	3	4	5	6	7
<i>Polytrichum longisetum</i>	5-	-	-	-	-	-	-
<i>Diplophyllum albicans</i>	2-	-	-	-	12-	-	-
<i>Dicranum polysetum</i>	2-	6-	-	-	-	-	-
<i>Ptilidium pulcherrimum</i>	-	6-	-	-	12-	-	-
<i>Eurhynchium praelongum</i>	-	6-	-	-	12-	-	-
<i>Peltigera canina</i>	-	6-	-	-	-	14-	-
<i>Hypnum cupressiforme</i>	-	-	5-	9-	-	-	-
<i>Sphagnum centrale</i>	2-	-	-	-	-	-	-
<i>Jungermannia hyalina</i>	2-	-	-	-	-	-	-
<i>Brachythecium salebrosum</i>	2-	-	-	-	-	-	-
<i>Ptilium crista-castrensis</i>	2-	-	-	-	-	-	-
<i>Sphagnum cuspidatum</i>	2-	-	-	-	-	-	-
<i>Cladonia gracilis</i>	2-	-	-	-	-	-	-
<i>Calypogeia</i> sp.	2-	-	-	-	-	-	-
<i>Lophocolea bidentata</i>	2-	-	-	-	-	-	-
<i>Calliergon stramineum</i>	2-	-	-	-	-	-	-
<i>Mnium stellare</i>	2-	-	-	-	-	-	-
<i>Atrichum undulatum</i>	-	6-	-	-	-	-	-
<i>Lophozia incisa</i>	-	6-	-	-	-	-	-
<i>Dicranella</i> sp.	-	6-	-	-	-	-	-
<i>Cephalozia</i> sp.	-	6-	-	-	-	-	-
<i>Ditrichum flexicaule</i>	-	6-	-	-	-	-	-
<i>Plagiomnium cuspidatum</i>	-	6-	-	-	-	-	-
<i>Cladonia squamosa</i>	-	6-	-	-	-	-	-
<i>Rhizocarpon geographicum</i>	-	6-	-	-	-	-	-
<i>Ptilidium ciliare</i>	-	6-	-	-	-	-	-
<i>Porella platyphylla</i>	-	6-	-	-	-	-	-
<i>Pogonatum urnigerum</i>	-	6-	-	-	-	-	-
<i>Racomitrium canescens</i>	-	6	-	-	-	-	-
<i>Cladonia bellidiflora</i>	-	6	-	-	-	-	-
<i>Eurhynchium bians</i>	-	-	-	9-	-	-	-
<i>Eurhynchium angustirete</i>	-	-	-	9-	-	-	-
<i>Pseudevernia furfuracea</i>	-	-	-	9-	-	-	-
<i>Alectoria</i> sp.	-	-	-	9-	-	-	-
<i>Drepanocladus uncinatus</i>	-	-	-	-	12-	-	-
<i>Eurhynchium</i> sp.	-	-	-	-	12-	-	-
<i>Nardia scalaris</i>	-	-	-	-	-	14-	-
<i>Hylocomium umbratum</i>	-	-	-	-	-	14-	-
<i>Scleropodium purum</i>	-	-	-	-	-	14-	-
<i>Sphagnum fuscum</i>	-	-	-	-	-	-	17-
<i>Dicranum fuscescens</i>	-	-	-	-	-	-	17-
<i>Pleuridium subulatum</i>	-	-	-	-	-	-	17-
<i>Polytrichum juniperinum</i>	-	-	-	-	-	-	17-
<i>Cephalozia lunulifolia</i>	-	-	-	-	-	-	17-
<i>Amblystegium serpens</i>	-	-	-	-	-	-	17-
<i>Sphagnum russowii</i>	-	-	-	-	-	-	17-
<i>Polytrichastrum alpinum</i>	-	-	-	-	-	-	17-
<i>Barbilophozia attenuata</i>	-	-	-	-	-	-	17-

*Sphagno [quinquefarii]-Piceetum* (Tx. 1937) Hartmann 1953 (Rec. 10C, cf. Kučera 2019b) [ $\equiv Piceetum excelsae sphagnetosum [quinquefarii]$  Tx. 1937],  
? *Hieracio transsilvanici-Piceetum* Pawłowski et Br.-Bl. in Br.-Bl. et al. 1939 p.p. min.,  
*Homogyno alpinae-Piceetum* Samek 1961 nom. superfl. (Art. 29c) p.p.,  
*Calamagrostio villosae-Piceetum* Hartmann et Jahn 1967 nom. illeg. (Art. 29c, 31) p.p. maj. (= excl.  
*Calamagrostio villosae-Piceetum sphagnetosum* Hartmann et Jahn 1967),  
? *Listero cordatae-Piceetum subalpinum* Mayer et Hofmann 1969 nom. illeg. (Art. 34a) p.p. min.  
*Homogyno alpinae-Piceetum* Zukrigl 1973 (sensu typus),  
*Plagiothecio-Piceetum tetricum* J. Matuszkiewicz 1977 nom. illeg. (Art. 34a) p.p.  $\equiv$  *Plagiothecio-Piceetum*  
(J. Matuszkiewicz 1977) J. Matuszkiewicz 2001 p.p.,  
*Vaccinio myrtilli-Piceetum* Sofron 1981 nom. inval. (Art. 5a) [nom. illeg. (Art. 31)], *Vaccinio*  
*vitis-idaeae-Piceetum* Kubíček et Šomšák 1993 nom. inval. (Art. 3b)  
Incl.: ? *Hieracio transsilvanici-Piceetum normale* Pawłowski et Walas 1949 nom. illeg. (Art. 13a), *Vaccinio*  
*myrtilli-Piceetum typicum* Šoltés 1976 p.p.  
Pseud.: *Piceetum myrtillosum* sensu Szafer et al. 1923 non Beger 1922 nom. inval. (Art. 3d) p.p., *Soldanello*  
*montanae-Piceetum* auct. non Volk in Braun-Blanquet et al. 1939 p.p. (see OBERDORFER 1957; SAMEK  
1961; OBERDORFER et al. 1967; WALLNÖFER 1993), *Calamagrostio villosae-Piceetum* auct. non Schlüter  
1966

Corresponding nomina ficta (phantom names): *Piceetum excelsae myrtilletosum* Szafer et al. 1923 apud auct.,  
*Piceetum excelsae carpathicum* (Szafer et al. 1923) Br.-Bl. et al. 1939 apud Celiński et Wojterski 1978,  
*Calamagrostio villosae-Piceetum* Hartmann 1953 apud auct. (HARTMANN & JAHN 1967; OBERDORFER  
et al. 1967; SOFRON 1981), *Calamagrostio villosae-Piceetum* (Tx. 1937) Hartmann ex Schlüter 1966  
apud Seibert 1992

Non: *Piceetum excelsae normale silicicolum* Sillinger 1933 nom. illeg. (Art. 34a), *Homogyno alpinae-Piceetum*  
Samek et al. 1957 (Rec. 10C, Art. 30a), *Luzulo sylvaticae-Piceetum* Wraber ex Wraber 1963, *Calamagrostio*  
*villosae-Piceetum* Schlüter 1966; *Listero cordatae-Piceetum subalpinum* Mayer et Hofmann 1969 nom.  
illeg. (Art. 34a) p.p. maj. (cf. *Listero cordatae-Piceetum* (Mayer et Hofmann 1969) Pignatti 1998 nom.  
inval. (Art. 3a)  $\equiv$  *Listero cordatae-Piceetum* (Mayer et Hofmann 1969) Pignatti et Pignatti 2014 nom.  
inval. (Art. 3i, 39b)

Set of the diagnostic species within the evaluated dataset:

E<sub>1</sub>: *Trientalis europaea*,

E<sub>0</sub>: –.

Relevé data: KRAJINA (1933), tab. 69, rels. 9, 11; SAMEK et al. (1957), tab. 15, rel. 34; LAKATOSOVÁ  
(1971), tab. 3, rels. 3, 12, 13; ŠOLTÉS (1976), tab. 4, rels. 3, 4, 11, 21; KOBZÁKOVÁ (1987) (msc.),  
tab. 6, rel. 15; MORAVČÍKOVÁ (1987) (msc.), tab. 2, rel. 9 and tab. 6, rel. 19; NAĎOVÁ (1987)  
(msc.), tab. 1, rels. 7, 11, 20, 29; RAJCOVÁ (1987) (msc.), tab. I.1, rels. 6, 16, 17, 19, 20, 22, 23,  
28, 30 and tab. I.3, rels. 2, 4; KUBÍČEK et al. (1992), tab. 1, rel. 2; ČERNUŠÁKOVÁ (1994), tab. 1,  
rel. 2, 3; KRAJČÍ (2009) (msc.), tab. 3, rels. 22, 24 and tab. 5, rel. 43 [cf. KRAJČÍ 2008]; KUČERA  
(2012a): 294–295, rels. 25–29; F. Máliš ined. (1 rel.). See fig. 2.

This association is the most widespread plant community of supramontane acid Norway spruce woodland in Central Europe developed on the non-carbonate rocks, typical especially for the mittelgebirge mountain ranges such as the Bavarian Forest, the Giant Mountains or the Veľká Fatra Mts. Its characteristic feature is a very low plant species diversity, therefore this community is floristically (mostly) negatively differentiated against other acid Norway spruce communities.

*Picea abies* is dominant and frequently the only species of the tree layer especially in phytocoenoses influenced by past land management (including historical deforestation). However, *Sorbus aucuparia* (usually ssp. *gabrata*) is also the natural component of stands, very often represented by rejuvenated individuals mostly with limited life span. In the Tatra region (and probably also in the Low Tatras), *Larix decidua* was native element of stands. The possibility of a natural *Abies alba* presence should be further studied (the species ascends in tree form also above 1500 m a.s.l.: cf. KUČERA 2012a, 2021)

In the understorey, presence of *Ribes petraeum* and *Lonicera nigra* was noted only sporadically, *Pinus mugo* is admixed in ecologically limit habitats. Only dwarf growth of *Acer pseudoplatanus*, *Fagus sylvatica* and *Pinus cembra* (only within the Tatra region) is considered for (sporadic) occurrences within this association, for the two former species exclusively in the lower altitudinal limit of the community.

Species composition of the field layer is very poor, not seldom consisting of 3–5 basic constantly accompanying species only. The most frequent dominant is *Vaccinium myrtillus*, in some cases could (co-)dominate some of the species *Homogyne alpina*, *Oxalis acetosella* and especially *Calamagrostis villosa*. Higher cover could be here and there reached by *Dryopteris dilatata*, *Luzula sylvatica* ssp. *sylvatica*, *D. expansa* or *Athyrium distentifolium*. The three species *V. myrtillus*, *C. villosa* and *A. distentifolium* usually form characteristic small-scale dominance mosaic pattern of the community field layer (TRAUTMANN 1952; PETERMANN et al. 1979; KUČERA 2012a). *Avenella flexuosa* is almost a constantly present species.

*Vaccinium vitis-idaea*, *Gentiana asclepiadea*, *Rubus idaeus*, (*Prenanthes purpurea*) belong to relative frequently admixed species. Other species are present in the stands of this association mostly sporadically, and generally with low cover-abundances, for example *Dryopteris carthusiana*, *Huperzia selago*, *Trientalis europaea*, *Maianthemum bifolium* etc., or species usually concentrated – within the group natural acid *Picea abies* associations – in other plant communities (*Adenostyles alliariae*, *Lycopodium annotinum*, *Luzula luzuloides*, *Senecio hercynicus*, *Stellaria nemorum* etc.). In the Tatra Mountains and the Low Tatras *Soldanella marmarossiensis* agg. grows abundantly here and there (a regional vicariant against woodlands of the north-eastern Alps and the Bohemian Forest with *Soldanella montana* Willd.: VALACHOVIČ et al. 2019).

*Dicranum scoparium* is the most frequent species of the ground layer; however, the layer dominant is most frequently *Polytrichum formosum* (cover more than 25–50%), but the latter species could also be absent. *Plagiothecium curvifolium* and *Pleurozium schreberi* belong among regularly present species, even if with lower constancy. Occasionally also other species grow in the stands (*Lepidozia reptans*, *Plagiomnium affine*, *Plagiothecium undulatum*, *Rhytidadelphus triquetrus* etc.). Some habitat types are characterized by the presence of *Sphagnum* species (usually with higher cover-abundance values), especially *S. girgensohnii* (often typically with *Polytrichum commune*); *S. capillifolium* and *S. quinquefarium* were noted less frequently.

Sample phytocoenosis (KRAJČÍ 2008, tab. 1, rel. 15, Low Tatras, 1440 m a.s.l.; for bryophytes see KRAJČÍ 2009):

E<sub>3</sub>: *Picea abies* 4,

E<sub>2</sub>: *Picea abies* 1,

- E<sub>1</sub>: *Vaccinium myrtillus* 3, *Calamagrostis villosa* 2, *Homogyne alpina* 2, *Oxalis acetosella* 2, *Avenella flexuosa* 1, *Dryopteris dilatata* 1, *Athyrium distentifolium* 1, *Luzula sylvatica* 1, *Soldanella marmarossiensis* agg. 1, *Gentiana asclepiadea* +, *Prenanthes purpurea* +,  
E<sub>0</sub>: *Polytrichum formosum* 2, *Plagiothecium curvifolium* 2, *Dicranum scoparium* 1, *Pleurozium schreberi* 1, *Plagiothecium undulatum* +.

This association is distributed throughout whole Central Europe in the Carpathian and the Hercynian mountain ranges (BRAUN-BLANQUET et al. 1939; KLIKA 1941 and later versions of this syntaxonomical summaries; OBERDORFER 1957; MATUSZKIEWICZ & MATUSZKIEWICZ 1960; HARTMANN & JAHN 1967; MATUSZKIEWICZ 1977, 2002; SEIBERT 1992; WALLNÖFER 1993; KASPROWICZ 1996; EXNER 2007; CHYTRÝ et al. 2013b); however, it is known under various names (see the nomenclatural note 1 below). EXNER (2007) mentions its rare occurrence within the Alps.

In relation to the distribution of *Lophozio-Piceetum* in the Slovak and Polish Western Carpathians, presence of this association is also possible within the Ukrainian Carpathians (cf. SHELYAG-SOSONKO et al. 2006; DUBYNA et al. 2019), but phytocoenological differences between the Eastern Carpathian and the Hercynian-Western Carpathian communities should be studied in more detail. However, the phytocoenosis documented by SOLOMAKHA et al. (2004) as a sample of the association *Calamagrostio villosae-Piceetum* comes from an anthropogenic Norway spruce forest of the class *Carpino-Fagetea*, most probably from the association *Calamagrostio villosae-Fagetum* Mikyška 1972 (cf. below the syntaxonomical note 3).

**Variability.** – The very low number of species commonly growing in the phytocoenoses of this association is reflected in very limited available floristical differentiation of the subcommunities developed in clearly distinct habitat types. In some cases only quantitative differences could be present. Therefore, even considerable small phytocoenotic (and/or floristical) differences have syntaxonomically sufficient ecological value.

The following subcommunities were only poorly documented from Slovakia, the typical subassociation being the only exception. In addition, a separate geographical variant of hochgebirge mountain ranges could be differentiated (probably within several following subunits, especially subassociation *typicum*) recognized by native occurrence of *Larix decidua*, *Athyrium filix-femina*, partially *Calamagrostis arundinacea* (*Dryopteris filix-mas*): presence of these species within montane *Picea* stands of mittelgebirge mountain ranges usually indicates plantations (*Larix*) or anthropogenic degraded *Carpino-Fagetea* communities (*Athyrium* etc.).

(1) The **subassociation *Lophozio-Piceetum typicum*** (first differentiated by TRAUTMANN [1952]; nomenclatural type: not selected [cf. TRAUTMANN 1952])<sup>3</sup> unites the typical, most common phytocoenoses of the association. Already TRAUTMANN (1952) called the attention to formation of characteristic small-scale dominance patterns of the field layer physiognomy made by species *Vaccinium myrtillus*, *Calamagrostis villosa* and *Athyrium distentifolium* within this subcommunity.<sup>4</sup> *V. vitis-idaea* reaches in the phytocoenoses only low cover-abundance values or is missing.

<sup>3</sup> Differential species: – ; syntax. syn.: *Soldanello-Piceetum barbilophozietosum* Oberdorfer 1957, *Calamagrostio villosae-Piceetum* Subassoziation nach *Lophozia floerkei* und *Lophozia lycopodioides* Hartmann et Jahn 1967 nom. superfl. (Art. 29c)/nom. illeg. (Art. 34c), *Calamagrostio villosae-Piceetum* typische Subassoziation (see HARTMANN & JAHN 1967).

<sup>4</sup> Careful differentiation of such respective small-scale *A. distentifolium* dominances and more species-rich as well as ecologically different woodlands of the association *Athyrio distentifolii-Piceetum* is necessary.

(2) Within the subassociation *Lophozio-Piceetum vaccinietosum vitis-idaeae* TRAUTMANN 1952 (nomenclatural type: not selected)<sup>5</sup>, there are delimited phytocoenoses occupying edaphically more extreme habitats, most commonly on steep, sun-exposed and quickly drying ± bouldery sites. They are characterized by a constant and more abundant presence of *Vaccinium vitis-idaea*, retreat of species demanding higher moisture and nutrient supply as well as by a constant occurrence of lichens and ecologically specific concentration of selected moss species to dry moss cushions, e.g. *Pleurozium schreberi* and *Hylocomium splendens* (TRAUTMANN 1952). Close related phytocoenoses were documented in Slovakia by KRAJINA (1933, tab. 69, rels. 9, 11) and KUBÍČEK & ŠOMŠÁK (1993, tab. 2, rel. 8).

(3) Within the subassociation *Lophozio-Piceetum sphagnetosum [quinquafarrii]* (Tx. 1937) P. Kučera 2023 comb. nov. hoc loco (Rec. 10C) (basionym: *Piceetum excelsae sphagnetosum [quinquafarrii]* Tx. 1937, published by TÜXEN (1937: 123) (cf. KUČERA 2019b: 321, 328, Suppl. A3: e7), nomenclatural type: not selected)<sup>6</sup> are comprised phytocoenoses of humid and cold, usually towards the north (to the east) oriented slopes. They are notable for numerous wet *Sphagnum* cushions (TÜXEN 1937); however, they do not create a dominant physiognomical feature of the phytocoenoses.

(4) The subassociation *Lophozio-Piceetum polytrichetosum communis* P. Kučera 2023 subass. nov. hoc loco (nomenclatural type: KUČERA (2012a): 295, rel. 29, holotypus hoc loco; original diagnosis: KUČERA (2019b): 294–295, rels. 26–29; differential species: *Polytrichum commune* [dom.], *Sphagnum girgensohnii* [dom.])<sup>7</sup> is here newly described for phytocoenoses of wet habitats which develop on very slightly inclined and plateau-like sites. They are characterized by a distinct development of the bryophyte cover with a larger number of represented species. Dominating species are *Polytrichum commune*, *Sphagnum girgensohnii* and *P. formosum*. *Avenella flexuosa* is missing in the hitherto known relevés.

(5) The other new subassociation *Lophozio-Piceetum nardetosum strictae* P. Kučera 2023 subass. nov. hoc loco (nomenclatural type: KUČERA (2012a): 312, rel. 78, holotypus hoc loco; original diagnosis: KUČERA (2012a): 312, rel. 78 + LEPŠ et al. (1985), tab. 1, rel. 6 + PETERMANN et al. (1979), tab. 3, rel. c8 + hochgebirge variant KRAJINA (1933), tab. 61, rel. 3, and tab. 64, rels. 3, 4, 6, 7; see also KUČERA (2012a): 293–294, rel. 24 and page 311, rels. 72–73 + HARTMANN & JAHN (1967), tab. 2, rels. 9, 13, 14) includes phytocoenoses similar to the subassociation *typicum*, however, with diagnostic species such as *Nardus stricta*, *Carex pilulifera*, *C. canescens*, partially *Deschampsia cespitosa* etc. (see TRAUTMANN 1952: 302), further *C. ovalis*, *Potentilla aurea*, *Agrostis capillaris*, *Hypericum maculatum*, *Bistorta major* or *Pulsatilla scherfelii*, *Anthoxanthum alpinum* etc. which are characteristic for habitats influenced by mountain pasture or complete past deforestation of the respective area (KRAJINA 1933; KUČERA, 2012a, 2019a).<sup>8</sup> These phytocoenoses

<sup>5</sup> Differential species: *Vaccinium vitis-idaea* (constant species); corresp. name: *Vaccinio vitis-idaeae-Piceetum* Kubíček et Šomšák 1993 nom. inval. (Art. 3b).

<sup>6</sup> Differential species: *Sphagnum* spp. (constant species); corresp. name: *Sphagno [quinquefarrii]-Piceetum* (Tx. 1937) Hartmann 1953, cf. KUČERA (2019b), non: *Calamagrostio villosae-Piceetum sphagnetosum* Hartmann et Jahn 1967.

<sup>7</sup> Original diagnosis: KUČERA (2012a): 294–295, rels. 27–29.

<sup>8</sup> However, *Nardus*, *Deschampsia* etc. could be natural components of *Lophozio-Piceetum* as well, for example on permanently wet habitats: such phytocoenoses do not belong to the *Lophozio-Piceetum nardetosum strictae*.

are already known from older studies, cf. constancy tables of BRAUN-BLANQUET et al. (1939) and TRAUTMANN (1952).

*Nomenclatural note 1.* – This community is known under various names in the Central European literature, initially as *Lophozio-Piceetum* (BRAUN-BLANQUET et al. 1939; KLIKA 1941; TRAUTMANN 1952; HARTMANN 1953) and *Piceetum hercynicum* Tx. in Br.-Bl. et al. 1939 (BRAUN-BLANQUET et al. 1939; KLIKA 1941; MATUSKIEWICZ & MATUSKIEWICZ 1960). In the later decades the name *Calamagrostio villosae-Piceetum*<sup>9</sup> Hartmann et Jahn 1967 came into use (HARTMANN & JAHN 1967; OBERDORFER et al. 1967; JIRÁSEK 1996, 2002; EXNER 2007; CHYTRÝ et al. 2013b); some authors used the name *Soldanello montanae-Piceetum* instead (OBERDORFER 1957; PETERMANN et al. 1979; WALLNÖFER 1993) – however, the respective name application was syntaxonomically incorrect (cf. KUČERA 2019b) which resulted in repeated pseudonymical use of the name (i.e. *Soldanello montanae-Piceetum* auct. non Volk in Braun-Blanquet et al. 1939).

The names *Plagiothecio-Piceetum hercynicum* and *Plagiothecio-Piceetum tetricum* are used in modern Polish literature for this community (cf. MATUSKIEWICZ 1977, 2002). Slovak authors use the name *Vaccinio myrtilli-Piceetum Šoltés* 1976 (cf. Šomšák in MUCINA et al. 1985; KANKA 2008; KUČERA 2012a) in accordance with the syntaxonomical survey of ŠOLTÉS (1976), or, alternatively, following the studies of Šomšák (cf. KUČERA 2012a: 243) the name *Calamagrostio villosae-Piceetum* is applied (simultaneously with the former name or exclusively the latter name) (Šomšák in MUCINA et al. 1985; JAROLÍMEK et al. 2008a).

Part of the authors prefer to use the name *Calamagrostio villosae-Piceetum* Hartmann et Jahn 1967 in the present (JIRÁSEK 2002; EXNER 2007; WILLNER 2007); however, KUČERA (2010a, 2012a) reminded that this name is an illegitimate name (Art. 31), because it is a younger homonym to the name *Calamagrostio villosae-Piceetum* Schlüter 1966 (used already by SEIBERT 1992: 69) and at the same time it is a superfluous name in relation to *Lophozio-Piceetum* Volk in Br.-Bl. et al. 1939 (Art. 29c, cf. HARTMANN & JAHN 1967).

The name *Calamagrostio villosae-Piceetum* Schlüter 1966 was recently accepted by CHYTRÝ et al. (2013b); however, the name *Lophozio-Piceetum* has to be prioritized for nomenclatural reasons (Moravec in JIRÁSEK 2002: 37; KUČERA 2012a). Moreover, the use of Schlüter's association name is problematic from the syntaxonomical point of view (see below).

*Nomenclatural note 2.* – Frequent application of '*Picea abies* syntaxa names' (and their original diagnoses) to natural (*Vaccinio-Piceetea*) as well as to anthropogenic Norway spruce phytocoenoses (*Carpino-Fagetea*) (see below) is the reason why numerous above-cited synonyms and other related syntaxa names are here preliminary cited as 'pro parte'-related names.

*Syntaxonomical note 1.* – The original description of the association *Lophozio-Piceetum* is based on the woodlands of the Bavarian Forest (BRAUN-BLANQUET et al. 1939; see the later studies of TRAUTMANN (1952), PETERMANN et al. (1979), EWALD et al. (2011) etc.). The Western Carpathian phytocoenoses of the association *Lophozio-Piceetum* differentiate phytochorologically only by a more infrequent presence of *Barbilophozia lycopodioides*, *Tribulus europaea* etc. as well as by the absence of *Soldanella montana* Willd. and *Galium saxatile*. However, the two latter species are not among frequent and distinctive species of the true supramontane Norway

<sup>9</sup> Either as nomen fictum *Calamagrostio villosae-Piceetum* Hartmann 1953 (and various fictitious author combinations) or later validly published as *Calamagrostio villosae-Piceetum* Hartmann et Jahn 1967.

spruce woodland even within the Bavarian Forest. These species differences could be evaluated as phytochorological variants within the association *Lophozio-Piceetum*.

*Syntaxonomical note 2.* – Careful consideration is required for the substantial differentiation of the associations *Lophozio-Piceetum* and *Athyrio distentifolii-Piceetum* (see below). Contrary to prevalent opinions, their phytocoenoses do not differ in the absence of poor abundance of *Athyrium distentifolium* (cf. SOFRON 1981; JIRÁSEK 1996; NEUHÄUSLOVÁ & ELTSOVA 2003; EXNER 2007; WILLNER et al. 2007; CHYTRÝ et al. 2013b: 374), but primarily in the group of differential species defined within the original description of *Athyrio distentifolii-Piceetum* (see HARTMANN & JAHN 1967, tab. 1).

The species *Athyrium distentifolium* is not mentioned within the original description of *Lophozio-Piceetum* (BRAUN-BLANQUET et al. 1939: 30–31); however, this case may be result of the specific approach of the authors of that study in respect of the compilation of their phytocoenological tables (see KUČERA 2008: 167). As could be clearly seen from the later studies from the Bavarian Forest (TRAUTMANN 1952; PETERMANN et al. 1979; EWALD et al. 2011), *A. distentifolium* is a regular component of the *Lophozio-Piceetum* phytocoenoses. Its cover-abundance within *Lophozio-Piceetum* could exceed even the value 25% (cf. KRAJČÍ 2008, tab. 2, rel. 30).<sup>10</sup>

Absence of *A. distentifolium* in the lower montane altitudes of the Central European mountain ranges is a typical attribute of the non-natural origin of the respective Norway spruce forest stands; larger areas of stands without *A. distentifolium* presence in the higher altitudes may indicate historical anthropogenic influences (deforestation in the deeper past).

*Syntaxonomical note 3.* – JIRÁSEK (1996) described the subassociation *Calamagrostio villosae-Piceetum fagetosum* Jirásek 1996 in which he included ‘climax montane communities distributed on the lower [altitudinal] limit of the climatic Norway spruce woodlands therefore the tree canopy is composed of prevailing *Picea abies* with admixture of *Fagus sylvatica* and *Abies alba*’ (cf. JIRÁSEK 2002; NEUHÄUSLOVÁ & ELTSOVA 2003). According to the recent field revisions, the respective documented forest stands are considered to represent anthropogenically changed phytocoenoses in habitats of the former natural mixed *Fagus* woodland (however, they were more frequently completely replaced by substitute *P. abies* forests).

The same evaluation can be applied to the unit *Calamagrostio villosae-Piceetum typicum* var. *calamagrostiosum arundinaceae* Jirásek 1996 (cf. KUČERA 2012a, 2013a, 2014), the phytocoenoses of which were incorrectly included by CHYTRÝ (2012) into a ‘mountain taiga’ (see above). Equivalently, questionable are numerous stands from the lower elevations documented for example by HUECK (1939), MATUSZKIEWICZ & MATUSZKIEWICZ (1960), HARTMANN & JAHN (1967), MIKYŠKA (1972), MATUSZKIEWICZ (1977) or SOFRON (1981) from the Hercynian and Western Carpathian mountain ranges, especially those indicated by presence of *Athyrium filix-femina*, *Calamagrostis arundinacea*, *Polygonatum verticillatum* or *Luzula pilosa*.<sup>11</sup>

<sup>10</sup> Full (but somewhat different) relevé version was given by KRAJČÍ (2009 msc.), tab. 5, rel. 43: E<sub>3</sub>: *Picea abies* 4, E<sub>2</sub>: *Picea abies* 2, E<sub>1</sub>: *Picea abies* +, *Sorbus aucuparia* +, *Vaccinium myrtillus* 3, *Athyrium distentifolium* 3, *Calamagrostis villosa* 2, *Homogyne alpina* 2, *Avenella flexuosa* 1, *Luzula sylvatica* 1, *Oxalis acetosella* 1, *Soldanella hungarica* +, E<sub>0</sub>: *Polytrichum formosum* 2, *Dicranum scoparium* 1, *Pleurozium schreberi* 1, *Plagiothecium curvifolium* +, *Plagiothecium undulatum* +.

<sup>11</sup> It should be noted that species as *Blechnum spicant*, *Streptopus amplexifolius* or *Trientalis europaea* are not exclusive species of natural Norway spruce woodlands within Central Europe (cf. SCHLÜTER 1969; MIKYŠKA 1972; NEUHÄUSLOVÁ & SOFRON 2005), instead, especially the first two could more frequently indicate the existence of former mixed *Fagus-Abies-Picea* forests of the class *Carpino-Fagetea*.

Also other selected Western Carpathian *Picea* forest stands with the species *A. flix-femina*, *C. arundinacea*, *Dryopteris filix-mas* from the altitudes ±1400–1450 m a.s.l. probably suggest the former existence of the upper montane woodland with *F. sylvatica* of the class *Carpino-Fagetea* (cf. KUČERA 2012a).

Moreover, the same evaluation is valid for substitute Norway spruce stands, in which centuries-long land management resulted in a total change of tree species composition and *Picea* is nowadays the only canopy species. This long-term anthropogenic impact may have influence on degradation of soil conditions and subsequent floristical change – resulting in development of plant assemblage resembling natural Norway spruce phytocoenoses from their lower altitudinal limit; however, this change is reversible. Such anthropogenic stands are usually notable for gradual secondary succession of *Fagus* (when a *Fagus* population was preserved in the vicinity) (KUČERA 2012a).

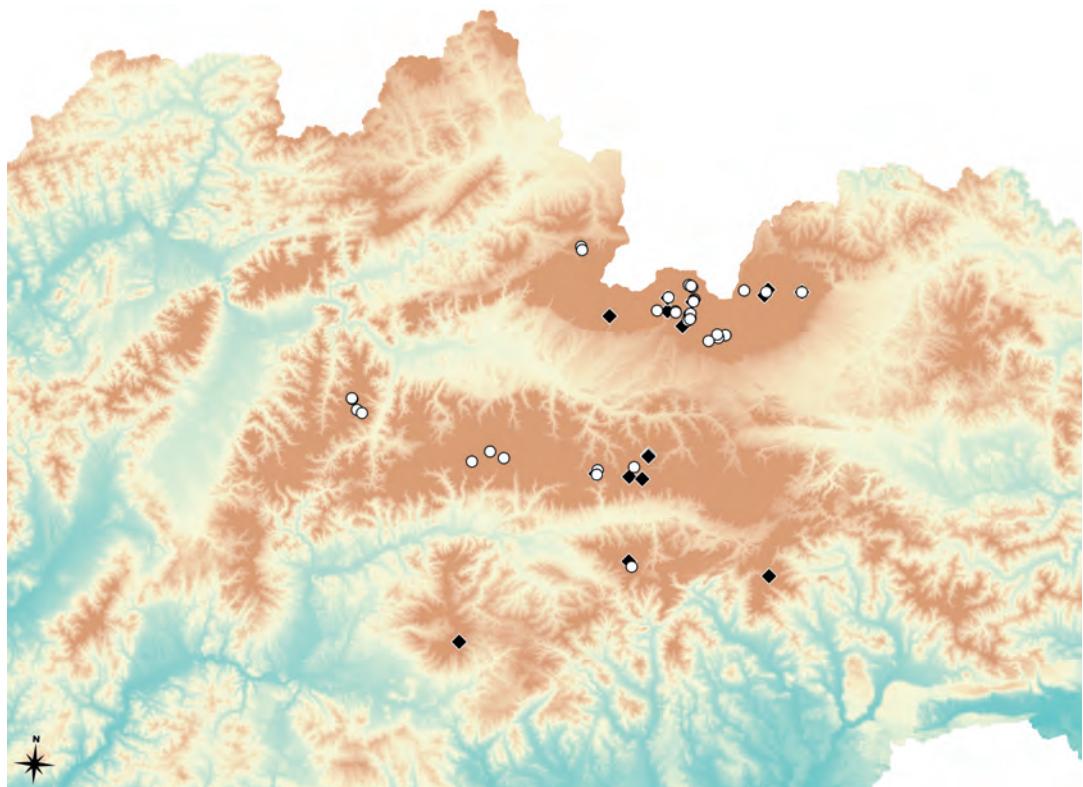
Further studies should question the possibility of differentiation of the above specified non-natural *Picea* and mixed *Picea* stands by means of their soil type: while podzols are typical of the true supramontane acid Norway spruce woodland, cambisols (cf. HARTMANN & JAHN 1967; JIRÁSEK 2002; CHYTRÝ et al. 2013b) could indicate sub-/anthropogenic *Picea* stands replacing the former mixed *Fagus* woodland and thus belonging to the class *Carpino-Fagetea* (cf. KUČERA 2022).

*Syntaxonomical note 4.* – The name *Calamagrostio villosae-Piceetum* Schlüter 1966 should not be treated as a syntaxonomical synonym to *Lophozio-Piceetum* Volk in Br-Bl. et al. 1939 (cf. KUČERA 2012a). Absence of species as *Athyrium distentifolium* or *Homogyne alpina* in the relevés of SCHLÜTER (1966, 1969) most probably indicate absence of real natural supramontane Norway spruce vegetation belt within the Thuringian Forest. The documented phytocoenoses are here considered for old anthropogenic Norway spruce stands originated upon centuries long land management (see also SCHLÜTER 1969: 158!), in the same manner as corresponding Western Carpathian stands. The name should be applied for species-poor substitute *Picea* forests of the order *Luzulo-Fagetalia sylvaticae* Scamoni et Passarge 1959 which replace original mixed *Fagus* woodland.

The species *Calamagrostis villosa* is not exclusively bound to natural Norway spruce woodland (cf. SCHLÜTER 1969; MIKYŠKA 1972; NEUHÄUSLOVÁ & SOFRON 2005), moreover, it should be noted that also *A. distentifolium* could be found as native species within upper montane *Fagus* phytocoenoses from the Black Forest (BARTSCH & BARTSCH 1940), the Sudetes (MIKYŠKA 1972) and the Bohemian Forest (NEUHÄUSLOVÁ & SOFRON 2005) to the Western Carpathians (KASPROWICZ 1996; UJHÁZYOVÁ et al. 2021; Kučera, not.).

*Syntaxonomical note 5.* – Recent Austrian authors included into the association *Lophozio-Piceetum* stands from the Alps with *Pinus cembra* and *Rhododendron ferrugineum* L. (EXNER 2007; see WILLNER et al. 2007, tab. 43; ut *Calamagrostio villosae-Piceetum*). However, the latter species is characteristic of syntaxa phytochorologically different from the whole Central European region. Moreover, *Pinus cembra* presence determines affiliation of the respective relevés to the alliance *Homogyno alpinæ-Pinion cembrae* P. Kučera 2017.

On the contrary, the presence of *Fagus sylvatica* within the relevés from the Bohemian Massif indicate that the authors – similarly as JIRÁSEK 1996 (see above note 3) – included in the respective dataset also the anthropogenic *Picea* phytocoenoses of the class *Carpino-Fagetea* (cf. KUČERA 2022).



**Figure 2.** Distribution of analysed relevés of the acid Norway spruce woodlands in Slovakia (central part): circles – *Lophozio-Piceetum*; diamonds – *Athyrio distentifolii-Piceetum*. Made with QGIS.

## 2.2. *Athyrio distentifolii-Piceetum abietis* Hartmann ex Hartmann et Jahn 1967 nom. corr.

Nomenclatural type: HARTMANN & JAHN (1967), tab. 1, rel. 27, lectotype (JIRÁSEK 1996: 250).

Original name: *Athyrio alpestris-Piceetum* F.K. Hartmann 1959 (HARTMANN & JAHN 1967: [15], 23, 381), i.e. *Athyrio alpestris-Piceetum abietis* Hartmann ex Hartmann et Jahn 1967 nom. incept. (Rec. 10C, Art. 44, Rec. 46D)

Syntax. syn.: *Athyrio alpestris-Piceetum* Hartmann ex Sýkora 1971 nom. illeg. (Art. 31)

Incl.: *Piceetum altherbosum* typ *Adenostyles alliariae* variant *silicolum* sensu Svoboda 1939 p.p., ? *Hieracio transsilvanici-Piceetum athyrietasum alpestris* Pawłowski et Walas 1949, *Homogyno-Piceetum athyrietasum alpestris* Samek et al. 1957 p.p. (Art. 14a, 30) = *Piceetum myrtilletosum athyrietasum alpestris* Samek et al. 1957 nom. inval. (čl. 3e, 4a) p.p., *Athyrio alpestris-Piceetum* Hartmann 1959 nom. nud. (Art. 2b), *Plagiothecio-Piceetum hercynicum filicetosum* J. Matuszkiewicz 1977 nom. illeg. (Art. 34a) p.p., *Plagiothecio-Piceetum tetricum filicetosum* J. Matuszkiewicz 1977 nom. illeg. (Art. 34a) p.p., *Piceetum excelsae carpaticum athyrietasum alpestris* Celiński et Wojterski 1978 p.p.

Pseud.: *Adenostylo-Piceetum* sensu Hartmann et Jahn 1967 non Hartmann 1953

Corresponding nomina ficta (phantom names): *Athyrio alpestris-Piceetum* Hartmann 1953 apud Hartmann et Jahn 1967 (only in tab. 1)

Non: *Piceetum altherbosum silicicolum* Sillinger 1933 nom. illeg. (Art. 13a, 34a); *Adenostylo-Piceetum* Hartmann 1953 [in relation to original diagnosis]; *Adenostylo alliariae-Piceetum* Zukrigl 1973 nom. illeg. (Art. 31); *Adenostylo-Piceetum* Ellenberg et Klötzli 1974 nom. illeg. (Art. 31)

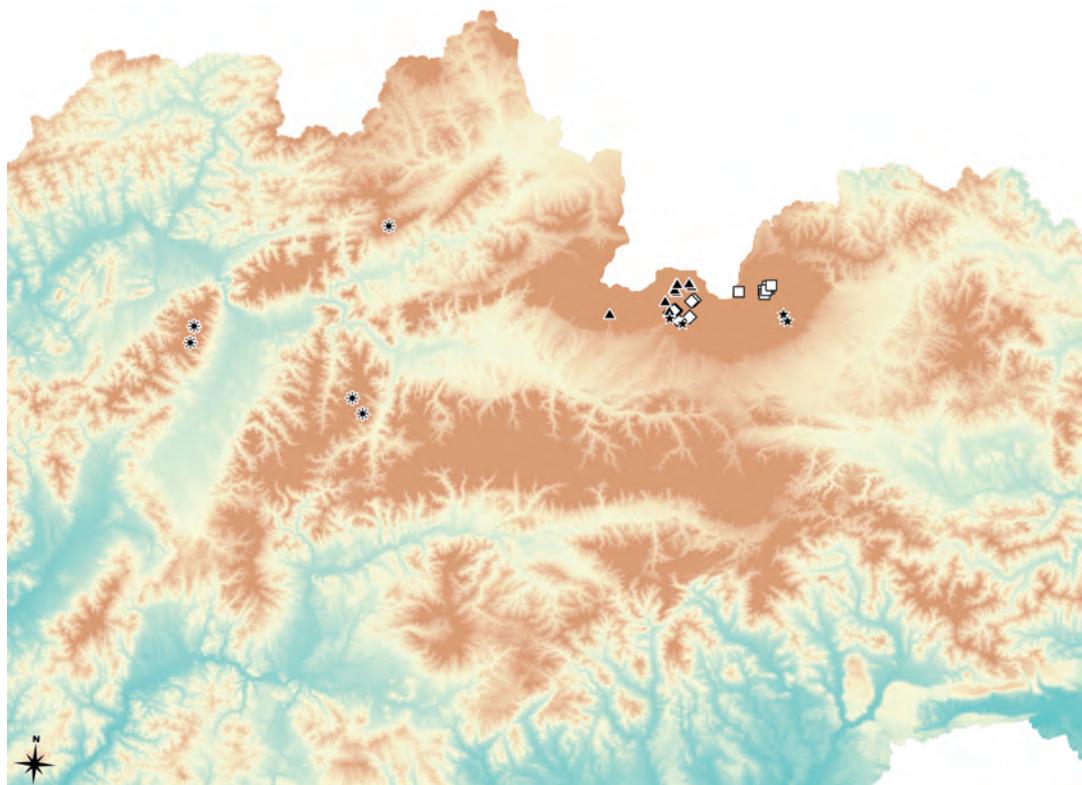


Figure 3. Distribution of analysed relevés of the acid Norway spruce woodlands in Slovakia (central part): diamonds – *Solidagini virgaureae-Piceetum*; triangles – *Parido quadrifoliae-Piceetum*; stars – *Lycopodio annotini-Sorbetum*; squares – *Listero cordatae-Piceetum*; asterisks – *Sphagno capillifolii-Piceetum*. Made with QGIS.

Set of the diagnostic species within the evaluated dataset:

$E_1$ : *Acetosa arifolia*, *Soldanella marmarossiensis* agg., *Milium effusum*, \**Stellaria nemorum*,  
 $E_0$ : –.

Relevé data: SAMEK et al. (1957), tab. 15, rels. 26, 37; ŠOLTÉS 1976, tab. 4, rel. 20; HORÁK (1971), tab. 1, rel. 6; NAĐOVÁ (1987, msc.), tab. 3, rels. 3, 8; RAJCOVÁ (1987, msc.), tab. I.3, rel. 6 and tab. I.6, rel. 1; KRAJČÍ (2009, msc.), tab. 3, rels. 11, 26 and tab. 5, rels. 45, 47, 50 [cf. KRAJČÍ 2008]; JANČOVIČOVÁ et al. (2011), tab. 2, rels. 2, 7; D. Miadok ined. (1 rel.). See Fig. 2.

This supramontane plant community is a typical companion of the association *Lophozio-Piceetum* – it replaces the latter unit on more humid and especially more trophically favourable habitats. It commonly develops on variable concave-shaped sites, where snow accumulates, as well as near slope springs (HARTMANN 1953, 1959; JIRÁSEK 1996).

The dominant canopy species *Picea abies* is regularly accompanied by *Sorbus aucuparia* (usually ssp. *glabrata*) though the spatial abundance pattern of the latter species is significantly influenced by impacts of historical land management in some areas (cf. the previous association). *Abies alba* probably entered the stands on the lower altitudinal limit of *Athyrio distentifolii-Piceetum* as a native species, *Fagus sylvatica* naturally occurs only rarely and only in shrubby growth.

*Pinus mugo* could be present in the understorey in some habitat types, sporadically *Lonicera nigra*, *Ribes petraeum* and *Sambucus racemosa* are present.

A substantial part of the constant species of the field layer corresponds to association *Lophozio-Piceetum* (*Oxalis acetosella*, *Vaccinium myrtillus*, *Homogyne alpina*, *Calamagrostis villosa* etc.). However, *Athyrio distentifolii-Piceetum* significantly differs by a set of differential species *Acetosa arifolia*, *Adenostyles alliariae* (within the subassociation *adenostylosum*), *Cicerbita alpina*, *Senecio hercynicus*, *Stellaria nemorum*, *Streptopus amplexifolius*, *Veratrum album* (ssp. *lobelianum* in the Western Carpathians) and others (cf. HARTMANN & JAHN 1967, tab. I and tab. II). *A. distentifolium* is a constant and usually markedly dominating species, *Vaccinium myrtillus* has lower cover-abundances in comparison to *Lophozio-Piceetum*. More frequent are *Luzula luzuloides* and *Prenanthes purpurea*. A weak positive differential species against the previous association is *Milium effusum*, *V. vitis-idaea* occurs, on the contrary, much scarcely. Less frequently grows also *Avenella flexuosa*.

The most frequent species of the ground layer are *Polytrichum formosum*, *Dicranum scoparium* and *Plagiothecium curvifolium*; the differentiation against *Lophozio-Piceetum* is only minimal. Relative less frequent are *Dicranum scoparium* and *Sphagnum* spp., on the contrary more abundant is *Rhizomnium punctatum* (cf. HARTMANN & JAHN, 1967; SÝKORA 1971; CHYTRÝ et al. 2013b).

Sample phytocoenosis (KRAJČÍ 2008, tab. 2, rel. 25, Low Tatras, 1 440 m a.s.l.; for bryophytes see KRAJČÍ 2009):

$E_3$ : *Picea abies* 4,

$E_1$ : *Picea abies* +, *Sorbus aucuparia* +,

*Athyrium distentifolium* 4, *Luzula sylvatica* 1, *Gentiana asclepiadea* 1, *Oxalis acetosella* 1, *Acetosa arifolia* +, *Adenostyles alliariae* +, *Dryopteris dilatata* +, *Gymnocarpium dryopteris* +, *Homogyne alpina* +, *Soldanella marmarossiensis* agg. +, *Stellaria nemorum* +, *Prenanthes purpurea* +, *Senecio nemorensis* agg. +, *Vaccinium myrtillus* +,

$E_0$ : *Pleurozium schreberi* 2, *Dicranum scoparium* 1, *Plagiomnium cuspidatum* 1, *Plagiothecium curvifolium* 1, *Rhytidadelphus squarrosus* +.

The association is widely distributed in Central Europe within the higher Hercynian mountain ranges (MATUSZKIEWICZ & MATUSZKIEWICZ 1960; HARTMANN & JAHN 1967; PETERMANN et al. 1979; JIRÁSEK 1996, 2002; EXNER 2007; CHYTRÝ et al. 2013b), existence of stands is also supposed in the Alps (EXNER 2007). Beside the distribution data from Slovakia, the community is documented from the Polish part of the Western Carpathians, too (RALSKI 1930; MATUSZKIEWICZ 1977; KASPROWICZ 1996).

With regard to relevé data of PAWŁOWSKI & WAŁAS (1949), the occurrence of *Athyrio distentifolii-Piceetum* might be deduced also within the northern Eastern Carpathians, but phytochorological differences between the Eastern Carpathian and the Hercynian-Western Carpathian communities should be studied in more detail. However, the recent documents on the distribution of the association within the Ukraine cited by DUBYNA et al. (2019) are partly examples of anthropogenically changed phytocoenoses of the class *Carpino-Fagetea* (cf. the syntaxonomical note 2 below).

**Variability.** – Phytocoenoses of the association are traditionally differentiated into two subcommunities. Part of the relevé samples from Slovakia do not represent their typical phytocoenotic development.

(1) The subassociation *Athyrio distentifolii-Piceetum typicum* (first differentiated by Hartmann & Jahn (1967); nomenclatural type: HARTMANN & JAHN (1967), tab. 1, rel. 27, automatical type

(cf. JIRÁSEK 1996: 254)<sup>12</sup> include typical stands of the association characteristically with striking dominance of *A. distentifolium*.

(2) The subassociation *Athyrio distentifolii-Piceetum adenostyletosum alliariae* Hartmann et Jahn 1967 (nomenclatural type: HARTMANN & JAHN (1967), tab. 1, rel. 1 (JIRÁSEK 1996: 255))<sup>13</sup> unites ± species-richer phytocoenoses on trophically more favourable habitats characterized by presence of *Adenostyles alliariae*, here and there even in subdominant abundance.

*Nomenclatural note 1.* – The name *Athyrio alpestris-Piceetum* was firstly introduced by HARTMANN (1959) – and validly published by HARTMANN & JAHN (1967) – who proposed this name as a replacement for his own older name *Adenostylo-Piceetum* Hartmann 1953. The latter name was only rarely used by later phytocoenologists, therefore WILLNER (2007) and later CHYTRÝ et al. (2013b) proposed the conservation of the name *Athyrio distentifolii-Piceetum* Hartmann ex Hartmann et Jahn 1967 [nom. corr.] as against *Adenostylo alliariae-Piceetum* Hartmann 1953 which is commonly considered to be an older synonym.

However, these two names are not syntaxonomical synonyms and there is no real need to propose conservation of *Athyrio distentifolii-Piceetum* Hartmann ex Hartmann et Jahn 1967 as against *Adenostylo-Piceetum* Hartmann 1953 (see summarization by KUČERA 2022: 132). The original diagnosis of the association *Adenostylo-Piceetum* Hartmann 1953 (HARTMANN 1953: Anhang, p. XIII) consists of three relevés of BARTSCH & BARTSCH (1940) originally classified as '*Luzulo nemorosae-Piceetum* (Schmid et Gaisberg 1936) Br.-Bl. et Sissingh in Br.-Bl. et al. 1939 *Luzula sylvatica*-Fazies' (see also WILLNER & ZUKRIGL 1999: 153). However, it should be noted that the characterization of the community in the text and table section of Hartmann's study does not correspond with the validly published part of the cited original diagnosis – i.e. HARTMANN (1953) used his own name as a pseudonym (KUČERA 2012a: 239–240). Following the original diagnosis,<sup>14</sup> the name *Adenostylo-Piceetum* Hartmann 1953 represents *Carpino-Fagetea* phytocoenoses with anthropogenically changed proportions of canopy species in favour of *Picea abies*:

*Adenostylo-Piceetum* Hartmann 1953 = *Luzulo luzuloidis-Piceetum* (Schmid et Gaisberg 1936) Br.-Bl. et Sissingh in Br.-Bl. et al. 1939 *Luzula sylvatica*-Fazies (sensu Bartsch et Bartsch 1940) = *Luzulo luzuloidis-Abietetum luzuletosum sylvaticae* Oberdorfer 1957 (see also KUČERA 2009a).

*Nomenclatural note 2.* – Similarly as mentioned above within the *Lophozio-Piceetum* subchapter, frequent application of syntaxa names which include anthropogenic Norway spruce phytocoenoses – correctly classified within the class *Carpino-Fagetea* (KUČERA 2012a, 2022) – is the reason why some of the above-cited synonyms and other related syntaxa names are here preliminary cited as 'pro parte'-related names.

*Syntaxonomical note.* – Phytocoenoses classified into the subassociation *Athyrio distentifolii-Piceetum athyrietasum filicis-feminae* Hartmann et Jahn 1967 (HARTMANN & JAHN 1967; JIRÁSEK 1996, 2002; NEUHÄUSLOVÁ & ELTSOVA 2003; CHYTRÝ et al. 2013b) or into the variant *Athyrio distentifolii-Piceetum typicum calamagrostiosum arundinaceae* Jirásek 1996 (JIRÁSEK 1996, 2002) are anthropogenically changed communities of the class *Carpino-Fagetea* (i.e. originally upper montane mixed *Fagus-Abies-Picea* communities), in which *Fagus* (eventually also *Acer*

<sup>12</sup> Without positive differential species.

<sup>13</sup> Differential species: *Adenostyles alliariae*.

<sup>14</sup> Nomenclatural type selected by KUČERA & KLIMENT (2011: 90).

*pseudoplatanus*) was not completely suppressed by historical land management. The same case represent the relevés originally assigned by SILLINGER (1933) into the subassociation *Piceetum altherbosum silicicolum* Sillinger 1933 (see also *Lophozio-Piceetum*, syntaxonomical note 3). Relevés of SEDLÁČKOVÁ (1978) directly indicate spontaneous reverse succession of *Fagus* within substitutionary *Picea* forests.

The rest of the original relevés of the association published by HARTMANN & JAHN (1967) should also be re-evaluated: they often represent anthropogenically changed *Carpino-Fagetea* communities, therefore, the authors' differentiation between *Athyrio distentifolii-Piceetum* and *Lophozio-Piceetum* (ut *Calamagrostio villosae-Piceetum*) was less exact.

It should also be noted that *A. distentifolium* could dominate the field layer even in the *Fagus* woodland as KASPROWICZ (1996) documented from the northern slopes of the Babia Góra Mt. massif, the central Western Beskids. Therefore, this species is not an exclusive distinguishing species of natural Norway spruce woodland within the forest stands.

The phytocoenotic delimitation of typically developed *Athyrio distentifolii-Piceetum* phytocoenoses was suitably narrowed by JIRÁSEK's (1996) choice of lectotype.

### 2.3. *Solidagini virgaureae-Piceetum abietis* P. Kučera et al. 2023

Nomenclatural type: Kučera et al. (2023), tab. 1, rel. 12, holotype (Kučera et al. 2023: in press).

Incl.: *Piceetum altherbosum* typ *Adenostyles alliariae* variant *silicicolum* sensu Svoboda 1939 p. p., *Adenostylo alliariae-Piceetum typicum* Šoltés 1976 p. p. min., spoločenstvo *Adenostyles alliariae-Picea abies* P. Kučera 2007 nom. ined. (Art. 1) p. p.

Pseud.: *Adenostylo-Piceetum* auct. slov. non Hartmann 1953 p. p. (see Kučera 2012a: 239)

Non: *Piceetum altherbosum silicicolum* Sillinger 1933 nom. illeg. (Art. 13a, 34a)

Set of the diagnostic species within the evaluated dataset:

E<sub>1</sub>: *Solidago virgaurea*, *Adenostyles alliariae*, *Hieracium murorum*, *Rubus idaeus*, \**Luzula luzuloides*, \**Senecio nemorensis* agg.,

E<sub>0</sub>: *Plagiothecium curvifolium*, *Chiloscyphus pallescens*.

Relevé data (cf. Kučera et al. 2023, tab. 1): MORAVČÍKOVÁ (1987, msc.), tab. 2, rel. 8 and tab. 4, rels. 5, 7, 9, 16, 19–21, 23, 26 and tab. 6, rels. 2–4, 10, 12–14, 17, 18; RAJCOVÁ (1987, msc.), tab. I.1, rels. 29, 35. See Fig. 3.

This natural acid Norway spruce community represents an ecological counterpart of the association *Athyrio distentifolii-Piceetum* as it is developed on sun-exposed steep slopes. Its original description has been recently published by Kučera et al. (2023). According to the current knowledge, distribution of the considered phytocoenoses is bound to the supramontane vegetation zone of hochgebirge mountain ranges, known localities were only documented from the Western Tatra Mts until now. Similar phytocoenoses in the Low Tatras (Kučera 2021, not.) should be studied in more detail.

The canopy of the hitherto known stands is shaped almost exclusively by *Picea abies*, only scarcely *Sorbus aucuparia* (ssp. *glabrata*) was noted. *Larix decidua* was probably a natural component of the canopy; however, the currently known relevés did not record this species. *Sorbus* samplings are constantly present in the stands.

In the understorey shrub, *Lonicera nigra*, *Ribes petraeum* and *Sambucus racemosa* are rarely present. The field layer is distinguished by set of constant species *Adenostyles alliariae*, *Solidago virgaurea*, *Senecio nemorensis* agg. (most probably *S. hercynicus*, cf. HODÁLOVÁ 1999), *Luzula luzuloides*; *Adenostyles* frequently with high cover-abundance values (even more than 50–75%). Less frequent significant species are *Calamagrostis arundinacea* (infrequently as a subdominant), *Athyrium filix-femina*, *Doronicum austriacum*, *Milium effusum*, *Cicerbita alpina* and *Hieracium murorum*: their presence in the habitats developed on non-carbonate rocks even in altitudes above 1500–1550 m a.s.l. distinctly contribute to a clear differentiation of *Solidagini-Piceetum* from the other natural Norway spruce phytocoenoses common in mittelgebirge mountain ranges (e.g. the Veľká Fatra Mts, the Western Beskids or the Bavarian Forest, the Giant Mountains).

The other species common in natural Norway spruce woodland are represented as well: *Vaccinium myrtillus*, *Oxalis acetosella*, *Homogyne alpina*, *Luzula sylvatica* ssp. *sylvatica*, *Dryopteris dilatata* [*D. expansa* was not recognized in the time of the field studies], *Gentiana asclepiadea*, here and there also *Calamagrostis villosa*; *V. vitis-idaea* is infrequent. *V. myrtillus*, *Oxalis* and *Calamagrostis* could reach cover-abundances between 25–50%. In contrast to *Athyrio distentifoli-Piceetum*, species typical for the latter unit such as *Athyrium distentifolium*, *Stellaria nemorum* or *Veratrum album* ssp. *lobelianum* are mostly absent in the hitherto documented relevés of *Solidagini-Piceetum*.

The most frequent species of the ground layer, occasionally with cover-abundance more than 5%, are *Plagiothecium curvifolium*, *Dicranum scoparium* and *Polytrichum formosum*. Other moss species have scattered occurrence, e.g. *Chiloscyphus pallescens*, *Plagiomnium affine*, *Pleurozium schreberi* etc.

Sample phytocoenosis (KUČERA et al. 2023, tab. 1, rel. 1, Western Tatra Mts, 1540 m a.s.l.):

E<sub>3</sub>: *Picea abies* 4,

E<sub>1</sub>: *Sorbus aucuparia* r,

*Adenostyles alliariae* 5, *Calamagrostis arundinacea* 2, *C. villosa* 2, *Senecio nemorensis* agg. 2, *Prenanthes purpurea* 2, *Homogyne alpina* 1, *Luzula luzuloides* 1, *Oxalis acetosella* 1, *Acetosa arifolia* +, *Avenella flexuosa* +, *Cicerbita alpina* r, *Doronicum austriacum* +, *Milium effusum* +, *Luzula sylvatica* +, *Rubus idaeus* +, *Vaccinium myrtillus* +, *Gentiana asclepiadea* r, *Ranunculus platanifolius* r,

E<sub>0</sub>: *Dicranum scoparium* +, *Plagiomnium affine* +, *Plagiothecium curvifolium* +.

The frequent dominant role of *Adenostyles alliariae* within *Solidagini virgaureae-Piceetum* is similar to phytocoenoses *Adenostylo alliariae-Piceetum abietis* Samek et al. 1957 nom. corr. et nom. cons. propos. (cf. KUČERA 2022); however, the latter community considerably differs by the presence of a group of calcareous and/or nutrient-demanding species (within the supramontane vegetation belt) (cf. KUČERA 2022).

*Syntaxonomical note 1.* – The synoptic table column of ‘*Piceetum altherbosum silicicolum* typ *Adenostyles alliariae*’ published by SILLINGER (1933: 96–98) consists of two relevés from which only the second one might possibly represent a natural Norway spruce stand (?); however, the exact location in the field and the respective species composition is uncertain. The column represents a mixture of phytocoenoses, therefore Sillinger’s name was not accepted as a corresponding name.

*Syntaxonomical note 2.* – The relevé of *Homogyno alpinae-Piceetum luzuletosum sylvaticae* Zukrigl 1973 *Adenostyles alliariae*-Variante published by ZUKRIGL (1973, tab. II) might represent a syntaxonomically related community to *Solidagini virgaureae-Piceetum*, though it comes from

a phytochorologically different area (the Eastern Alps) than the Hercynian-Western Carpathian region. The Gleinalpe, the Koralpe and the Tatra Mountains have their hochgebirge landform character in common; however, a more detailed comparison of the respective units is difficult due to the small number of documented relevés.

#### **2.4. *Parido quadrifoliae-Piceetum abietis* P. Kučera et al. 2023**

Nomenclatural type: KUČERA et al. (2023), tab. 1, rel. 27, holotype (KUČERA et al. 2023: in press).

Set of the diagnostic species within the evaluated dataset:

(E<sub>3</sub>: *Larix decidua*),

E<sub>1</sub>: *Melampyrum sylvaticum*, *Paris quadrifolia*, *Epilobium montanum*, *Blechnum spicant*, *Chaerophyllum hirsutum*, *Galeobdolon montanum*, *Luzula pilosa*, \**Stellaria nemorum*, \**Luzula luzuloides*, \**Calamagrostis arundinacea*, \**Athyrium filix-femina*, \**Senecio nemorensis* agg., E<sub>0</sub>: *Plagiochila poreloides*, *Plagiomnium undulatum*, *Sphagnum girgensohnii*.

Relevé data (cf. KUČERA et al. 2023, tab. 1): HORÁK (1971), tab. 1, rel. 5; NAĎOVÁ (1987, msc.), tab. 1, rels. 13, 14, 17–19, 25, 27, 30 and tab. 3, rels. 2, 6. See Fig. 3.

This recently distinguished association was described for another natural supramontane acid Norway spruce woodland plant community with a hochgebirge distribution pattern (KUČERA et al. 2023) – currently known localities were only documented from the Western Tatra Mts. The unit comprises relatively nutrient rich and humid acid *Picea* phytocoenoses floristically and ecologically different from all previous associations.

By the limited current knowledge, the canopy of the stands is dominated by *Picea abies*, sometimes admixed with both *Larix decidua* and *Sorbus aucuparia* (ssp. *glabrata*).

*Lonicera nigra* was sparsely documented in the understorey, *Pinus mugo* grows in some localities.

The field layer of the typical stands is characterized by the co-occurrence of more nutrient-demanding species as *Stellaria nemorum*, *Paris quadrifolia*, *Athyrium filix-femina*, *Senecio nemorensis* agg. (most probably *S. hercynicus*, cf. HODÁLOVÁ 1999), *Calamagrostis arundinacea*, accompanied by *Luzula luzuloides*, *Melampyrum sylvaticum* and *Vaccinium vitis-idaea*. *Epilobium montanum* and *Blechnum spicant* grow less frequently, examples of rarer species are *Galeobdolon montanum*, *Chaerophyllum hirsutum* or *Luzula pilosa*.

The dominant field layer species is usually *Vaccinium myrtillus*, accompanied by common species of Western Carpathian species of montane woodlands: *Homogyne alpina*, *Luzula sylvatica* ssp. *sylvatica*, *Oxalis acetosella* (subdominant), *Calamagrostis villosa*. Rarely *Dryopteris carthusiana* or *D. dilatata* could become dominants of the field layer [*D. expansa* was not recognized in the time of the field study].

Differential species of the ground layer are *Plagiochila poreloides* and *Sphagnum girgensohnii*, together with less frequent *Plagiomnium undulatum*. Common forest species as *Dicranum scoparium* and *Polytrichum formosum* belong to constant species, less frequently also *Hylocomium splendens* or *Plagiomnium affine* were found.

Sample phytocoenosis (KUČERA et al. 2023, tab. 1, rel. 26, Western Tatra Mts, 1470 m a.s.l.):

E<sub>3</sub>: *Picea abies* 4, *Larix decidua* r,

E<sub>2</sub>: *Picea abies* +,

- E<sub>1</sub>: *Picea abies* +, *Lonicera nigra* r, *Sorbus aucuparia* r,  
*Calamagrostis villosa* 2, *Vaccinium myrtillus* 2, *Calamagrostis arundinacea* 1, *Homogyne alpina* 1,  
*Oxalis acetosella* 1, *Athyrium filix-femina* +, *Avenella flexuosa* +, *Chaerophyllum hirsutum* +, *Luzula luzuloides* +, *L sylvatica* +, *Stellaria nemorum* +, *Senecio nemorensis* agg. +, *Vaccinium vitis-idaea* +, *Epilobium montanum* r, *Melampyrum sylvaticum* r, *Paris quadrifolia* r, *Prenanthes purpurea* r,  
E<sub>0</sub>: *Dicranum scoparium* 1, *Plagiochila poreloides* +, *Plagiomnium affine* +, *Polytrichum formosum* +, *Sphagnum girgensohnii* +.

*Syntaxonomical note.* – Small total number of the hitherto documented relevés does not allow the comprehensive evaluation of the phytocoenotic amplitude and the variability of *Parido quadrifoliae-Piceetum*. As typical phytocoenoses are considered stands with presence of *Melampyrum sylvaticum*, *Stellaria nemorum* and *Paris quadrifolia*. A part of the relevés assigned to this association lack these species; however, the presence of *Athyrium filix-femina* and *Calamagrostis arundinacea* and absence of differential species of the association *Solidagini virgaureae-Piceetum* indicate that the mentioned relevés most probably represent a variation of the association *Parido quadrifoliae-Piceetum*.

Further studies should resolve the question of syntaxonomical position of the special relevé of KOBZÁKOVÁ (1987, tab. 6, rel. 15; currently classified within *Lophozio-Piceetum*) – *Vaccinium vitis-idaea* cover-abundance value is '3' – with *Melampyrum*, *Luzula luzuloides*, *C. arundinacea*, *S. nemorensis* agg., but with absence of other species of this community.

## 2.5. *Lycopodio annotini-Sorbetum aucupariae* P. Kučera ass. nov. hoc loco

Nomenclatural type: ŠOLTÉS (1976), tab. 4, rel. 30, holotypus hoc loco.

Non: *Piceo abietis-Sorbetum aucupariae* Oberdorfer 1978, *Athyrio-Sorbetum* Borysiak 1984

Set of the diagnostic species within the evaluated dataset:

E<sub>3</sub>: *Betula carpatica*,

E<sub>1</sub>: *Lonicera nigra*,

*Gymnocarpium dryopteris*, *Hylotelephium argutum*, *Dryopteris filix-mas*, *Doronicum austriacum*, *Prenanthes purpurea*, *Ranunculus platanifolius*, \**Calamagrostis arundinacea*, \**Athyrium filix-femina*, \**Lycopodium annotinum*, \**Senecio nemorensis* agg.,

E<sub>0</sub>: *Sphenolobus minutus*, *Lophozia cf. incisa*, *Plagiothecium denticulatum*, *Tortella tortuosa*, *Tetraphis pellucida*, *Blepharostoma trichophyllum*, *Mnium* sp., \**Hylocomium splendens*, \**Rhytidiodelphus triquetrus*, \**Plagiochila asplenoides*.

Relevé data and original diagnosis: LAKATOSOVÁ (1971, msc.), tab. 3, rel. 10; ŠOLTÉS (1976), tab. 4, rels. 25–28, 30, 34; MORAVČÍKOVÁ (1987, msc.), tab. 17, rel. 1. See Fig. 3.

Occurrence of this community is usually bound to old windthrows in the supramontane (to montane?) vegetation zone in the region of the High Tatras; as typically developed phytocoenoses are here considered those occupying a scree habitat. The age of documented stands was 18–55 years (ŠOLTÉS 1976).

In contrast to the previous communities, the dominant species of the canopy is most frequently *Sorbus aucuparia* (ssp. *aucuparia*; cf. ŠOLTÉS 1969; DZUBINOVÁ et al. 1971) and *Picea abies* is either only admixed (eventually missing) or gradually superseding the former species. Other tree species in stands are *Betula carpatica*, *Larix decidua*, *Salix caprea*, eventually *Abies alba* and probably also *Acer pseudoplatanus* as (historically) indigenous species.

In the understorey *Lonicera nigra*, *Salix silesiaca* and, eventually, *Pinus mugo* are present.

A characteristic feature of the field layer is the presence of *Gymnocarpium dryopteris*, *Hylotelephium argutum*, *Lycopodium annotinum* (with variable frequency in the hitherto known relevés) along with the group of more or less constant species as *Athyrium filix-femina*, *Calamagrostis arundinacea*, *Prenanthes purpurea*, *Senecio nemorensis* agg., *Rubus idaeus*. Other (mostly) constant species contributing to the physiognomical appearance are common species of mountain woodlands as *Homogyne alpina*, *Avenella flexuosa*, *Dryopteris dilatata*, *Vaccinium myrtillus*, *Luzula sylvatica* ssp. *sylvatica* and *Gentiana asclepiadea*; *Calamagrostis villosa* has lower frequency, while *C. arundinacea* gained (sub)dominant role in some phytocoenoses within the relevés classified here. *Adenostyles alliariae*, *Cicerbita alpina*, *Doronicum austriacum*, *Dryopteris filix-mas*, *Veratrum album* subsp. *lobelianum* etc. belong to less frequent species.

Relevés with the group of ground layer species *Blepharostoma trichophyllum*, *Lophozia cf. incisa* [R. Šoltés, in e-mail, for all occurrences within his relevés in the association], *Plagiothecium denticulatum*, *Sphenolobus minutus*, *Tetraphis pellucida* and *Tortella tortuosa* are here considered to represent typical phytocoenoses which significantly differ from other natural acid Norway spruce communities; with addition of constant as well as characteristic species *Hylocomium splendens* and *Rhytidadelphus triquetrus* which indicate specific and ecologically distinct habitat types. Other common companions are *Dicranum scoparium* and *Polytrichum formosum*, *Pleurozium schreberi* grows with lower frequency.

Sample phytocoenosis (Šoltés 1976, tab. 4, rel. 28, High Tatras, 1 415 m a.s.l., windthrow site):

E<sub>3</sub>: *Sorbus aucuparia* 5, *Betula carpatica* +, *Picea abies* +,

E<sub>2</sub>: *Picea abies* 1, *Abies alba* + [planted: Šoltés 1969],

E<sub>1</sub>: *Abies alba* + [planted: Šoltés 1969], *Picea abies* +, *Sorbus aucuparia* r,

*Avenella flexuosa* 2, *Calamagrostis villosa* 2, *Dryopteris dilatata* 2, *Homogyne alpina* 2, *C. arundinacea* 1, *Senecio nemorensis* agg. 1, *Vaccinium myrtillus* 1, *Athyrium filix-femina* +, *Chamerion angustifolium* +, *Dryopteris filix-mas* +, *Hylotelephium argutum* +, *Lycopodium annotinum* +, *Rubus idaeus* +, *Veratrum album* ssp. *lobelianum* +, *Cicerbita alpina* r, *Prenanthes purpurea* r,

E<sub>0</sub>: *Polytrichum formosum* 2, *Blepharostoma trichophyllum* +, *Dicranum scoparium* +, *Hylocomium splendens* +, *Lophozia cf. incisa* + [R. Šoltés, in e-mail], *Plagiothecium denticulatum* +, *Pleurozium schreberi* +, *Rhytidadelphus triquetrus* +, *Tetraphis pellucida* +, *Tortella tortuosa* +.

The hitherto known relevés of the association were documented mainly from the High Tatras, therefore it is possible that *Lycopodium annotini-Sorbetum* could represent another type of community regionally limited to hochgebirge mountain ranges of the Western Carpathians. Physiognomically similar *Sorbus* communities in old windthrows from the Veľká Fatra Mts, Oravské Beskydy Mts etc. have a species composition similar to woodland types of *Lophozio-Piceetum* or, eventually, *Athyrio distentifolii-Piceetum* (see below).

*Syntaxonomical note 1.* – The existence and the development of natural *Picea abies* woodland is inseparably connected with small- or large-scale natural disturbances caused by wind storms (and frequently by subsequent outbreak of phloemophagous insects) (cf. HEURICH 2001; MÁLIŠ et al. 2015; NOVÁKOVÁ & EDWARD-JONÁŠOVÁ 2015; JANDA et al. 2017; ČERVENKA et al. 2019 etc.). The first more or less ‘forest phase’ of a series of secondary succession stages developed on *Picea* forest windthrows is frequently formed by temporary (up to several decades) stands with prevailing *Sorbus aucuparia*. However, their overall floristical composition mostly does not

considerably differ from the respective disturbed *Picea* community, therefore such phytocoenoses should be classified within that community. For example *Athyrio-Sorbetum* Borysiak 1984 stands from the Babia Góra Mt. represent at least partly a secondary succession variant of *Athyrio distentifolii-Piceetum*.

In this respect and according to the current knowledge, plant species composition of *Lycopodio annotini-Sorbetum aucupariae* phytocoenoses – especially ground layer species – represent a distinct syntaxon from other communities evaluated here. Further field studies should bring more data on *Sorbus*-dominated stands of the Tatra Mountains (as well as of the Low Tatra Mts) to a more accurate discrimination of *Lycopodio annotini-Sorbetum* and temporary *Sorbus*-phases of *Solidagini virgaureae-Piceetum* and *Parido quadrifoliae-Piceetum* as well as possible re-evaluation of here classified relevés.

*Syntaxonomical note 2.* – Especially the low total number of known phytosociological relevés is the reason why their overall floristical composition and mutual differences between them might appear unbalanced. For example two relevés of ŠOLTÉS (1976, tab. 4, rels. 25, 26) were originally classified into the cluster of *Parido quadrifoliae-Piceetum* in the final version of statistical classification. However, in respect of the presence of *Blepharostoma trichophyllum*, *Lophozia cf. incisa*, *Plagiothecium denticulatum*, *Sphenolobus minutus*, *Tetraphis pellucida* or *Hylocomium splendens*, I have moved them into *Lycopodio annotini-Sorbetum* and thus I followed the pre-final version of statistical comparison which included both field and ground layer species.

*Syntaxonomical note 3.* – OBERDORFER (1973) described within the alliance *Sambuco-Salicion capreae* the association *Piceo abietis-Sorbetum aucupariae* Oberdorfer 1973 which is also characterized by the dominance of *Sorbus aucuparia* (cf. OBERDORFER 1978; EXNER & WILLNER 2007). The community was primarily defined for relative species-poor montane phytocoenoses developing on clearcuts and other harvested sites as well as thinned sites within non-carbonate *Fagus* and [anthropogenic] *Picea* forests. This community significantly differs floristically, ecologically and altitudinally from *Lycopodio annotini-Sorbetum*.

SÁDLO et al. (2013) classified within *Piceo abietis-Sorbetum* also floristically and by their origin different phytocoenoses developing by means of secondary succession on anthropogenic non-forest habitats (cf. *Calamagrostis villosa*, *Holcus* spp., *Nardus stricta*). Similarly, VALACHOVIČ & HEGEDÜŠOVÁ (2020) included into that association the entirely phytocoenotically unrelated relevé of succession *Sorbus* stands which gradually overgrow the former mountain pastures of Flochová Mt., the Kremnické Vrchy Mts. Together with the *Picea-Sorbus-Fagus* relevé of KUČERA (2012a: 132), these two relevés are components of secondary succession series heading towards the re-establishment of an upper montane woodland of the alliance *Luzulo-Fagion* Lohmeyer et Tx. in Tx. 1954, phytocoenologically similar to phytocoenoses in the wider surroundings of the mountain top of Vtáčnik Mt. and primarily also Predná Poľana Mt. (KUČERA 2012a).

## 2.6. *Listero cordatae-Piceetum abietis* (Samek et al. 1957) P. Kučera 2023 comb. nov. hoc loco

Nomenclatural type: SAMEK et al. (1957), tab. 15, rel. 35, holotypus hoc loco.

Basionym: *Homogyno-Piceetum sphagnetosum acutifolii* Samek et al. 1957 (Art. 14a, 30) ≡ *Piceetum myrtilletosum sphagnetosum acutifolii* Samek et al. 1957 nom inval. (Art. 3e, 4a) (SAMEK et al. 1957: 18)

Incl.: ? *Piceetum excelsae myrtilletosum* Pawłowski ex Pawłowski et al. 1928 nom. illeg. (čl. 14b, 31) p. p.  
(i.e. Pawłowski et al. (1928), tab. XII, rel. 3), ? *Hieracio transsilvanici-Piceetum vaccinietosum myrtilli*  
Pawłowski et Walas 1949

Non: *Lycopodio-Piceetum montanum* Stefanović et Popović 1961 nom. nud. (Art. 2b), *Lycopodio-Piceetum montanum* Stefanović et Popović ex Stefanović 1964 nom. illeg. (Art. 34a), *Lycopodio annotini-Piceetum Faliński* 1965 nom. superfl. (Art. 29c), *Lycopodio annotini-Piceetum* W. Matuszkiewicz et al. 1994 nom. inval. (čl. 3b);

*Listero cordatae-Piceetum subalpinum* Mayer et Hofmann 1969 nom. illeg. (Art. 34a) (cf. *Listero cordatae-Piceetum* (Mayer et Hofmann 1969) Pignatti 1998 nom. inval. (Art. 3a) ≡ *Listero cordatae-Piceetum* (Mayer et Hofmann 1969) Pignatti et Pignatti 2014 nom. inval. (Art. 3i, 39b)

Set of the diagnostic species within the evaluated dataset:

E<sub>1</sub>: *Listera cordata*, *Huperzia selago*, *Veratrum album* ssp. *lobelianum*, \**Lycopodium annotinum*,  
\**Athyrium distentifolium*,

E<sub>0</sub>: *Bazzania trilobata*, *Calypogeia azurea*, *Cladonia* sp., *Pleurozium schreberi*, *Barbilophozia lycopodioides*, *Sphagnum recurvum* agg., *Rhytidiodelphus squarrosus*, *Schistidium apocarpum*, *Plagiothecium undulatum*, *Plagiothecium laetum*, \**Hylocomium splendens*, \**Rhytidiodelphus triquetrus*, \**Plagiochila asplenioides*, \**Sphagnum capillifolium*.

Relevé data and original diagnosis: SAMEK et al. (1957), tab. 15, rels. 20, 24, 31, 33, 35, 38; JASÍK & DÍTĚ (2016): 11, rel. 2. See Fig. 3.

This montane to supramontane Norway spruce community is limited to stony and bouldery habitats, i.e. to small- or larger-sized screes, with inter-boulder places filled with raw humus. Such habitats are frequently found on steep slopes with seeping water (SAMEK et al. 1957); commonly on colder, from the north-west to the east oriented slope expositions.

*Picea abies* dominates in the stands of this association, *Sorbus aucuparia* could be admixed; both species regularly rejuvenate; sporadic occurrence of *Salix silexiaca*.

*Pinus mugo* grows in the understorey on some localities, eventually with higher cover-abundance.

The bouldery habitat is in the field layer expressed by the frequent presence of *Lycopodium annotinum*, *Huperzia selago* and (less frequently documented) *Gymnocarpium dryopteris*. The relict character of the phytocoenoses is represented by the constant presence of *Listera cordata* as well as by the unique occurrence of *Linnaea borealis* – a very rare species within the Western Carpathians (cf. JASÍK et al. 2014; JASÍK & DÍTĚ 2016).

The dominant species of the field layer is *Vaccinium myrtillus*, with constant companions *Oxalis acetosella*, *Homogyne alpina* (both occasionally with cover-abundance more than 5%), *Dryopteris carthusiana*, *Avenella flexuosa*. The special habitat type forces significant limitation of cover-abundance values of other more or less constant species *Athyrium distentifolium*, *Calamagrostis villosa* or *Luzula sylvatica* ssp. *sylvatica*. Among the less frequent species are *Gentiana asclepiadea*, *Veratrum album* ssp. *lobelianum*, sporadically *Adenostyles alliariae*, *Valeriana tripteris* or *Ligusticum mutellina*, *Gentiana punctata* are documented.

Cover of the ground layer species reaches high cover-abundances in the phytocoenoses (usually more than 70%). Peat moss clusters or cushions (*Sphagnum capillifolium*, *S. cf. fallax* [ut *S. recurvum*]) are found in small depressions, while wet boulders are overgrown by blankets of *Plagiothecium undulatum*, *Rhytidiodelphus triquetrus* etc. (SAMEK et al. 1957). Constant species

(partly with higher cover) are *Dicranum scoparium*, *Polytrichum formosum*, *Hylocomium splendens* or *Pleurozium schreberi*. Higher frequency also have *Barbilophozia lycopodioides*, *Calypogeia azurea*, infrequently are documented hitherto *Bazzania trilobata*, *Plagiochila asplenoides*, *R. squarrosus* etc., including lichens (*Cetraria islandica*, *Cladonia* sp.).

Sample phytocoenosis (SAMEK et al. 1957, tab. 15, rel. 20, High Tatras, 1300 m a.s.l.):

E<sub>3</sub>: *Picea abies* 5,

E<sub>1</sub>: *Picea abies* +, *Sorbus aucuparia* +,

*Vaccinium myrtillus* 4, *Homogyne alpina* 2, *Oxalis acetosella* 2, *Athyrium distentifolium* 1, *Avenella flexuosa* +, *Calamagrostis villosa* +, *Dryopteris carthusiana* +, *Gymnocarpium dryopteris* +, *Huperzia selago* +, *Lycopodium annotinum* +, *Luzula sylvatica* +, *Listera cordata* +, *Phegopteris connectilis* +, *Solidago virgaurea* +, *Veratrum album* ssp. *lobelianum* +,

E<sub>0</sub>: *Polytrichum formosum* 4, *Sphagnum capillifolium* 2, *Plagiothecium undulatum* 2, *Barbilophozia lycopodioides* 1, *Dicranum scoparium* 1, *Hylocomium splendens* 1, *Pleurozium schreberi* 1, *Scleropodium purum* 1, *Bazzania trilobata* +, *Lepidozia reptans* +, *Cladonia* sp. +, *Peltigera canina* +, *Plagiochila asplenoides* +, *Plagiothecium laetum* +, *Rhytidiodelphus squarrosus* +, *R. triquetrus* +, *Tetraphis pellucida* +.

The relevés of *Listero cordatae-Piceetum* were documented hitherto from the northern part of the High Tatras (cf. SAMEK et al. 1957; JASÍK & DÍTĚ 2016); a corresponding habitat or phytocoenosis were not documented from the mittelgebirge mountain ranges of the Western Carpathians till now. Relevés classified by SOFRON (1976) under the association name *Anastrepto-Piceetum* Stöcker 1967 might also marginally belong to *Listero cordatae-Piceetum*, likewise the scree phytocoenoses from the Ukrainian Gorgany Mts documented by IAKUSHENKO et al. (2006: ‘*Luzulo-Piceetum sphagnetosum*’).

*Taxonomical note.* – SAMEK et al. (1957) listed *Sphagnum recurvum* within the stands of *Listero cordatae-Piceetum*. However, this species does not occur in Europe (FLATBERG 1992); probably *S. fallax* grows in the respective sites. Record of *S. girgensohnii* domination by JASÍK & DÍTĚ (2016, rel. 2) may be problematic as well.

*Nomenclatural note.* – PIGNATTI (1998: 141) included in the synonymy of the association *Homogyno alpinæ-Piceetum* Zukrigl 1973 the name ‘*Listero-Piceetum* Mayer (1969)’, without a reference to the original publication of MAYER & HOFMANN (1969), where the original name *Listero-Piceetum subalpinum* was published. Pignatti’s name might be viewed as a nomen novum (Art. 39b) but the more appropriate evaluation is that it represents an inaccurate adoption of the older name, i.e. a fictitious name (nomen fictum or ‘phantom name’) as Mayer et Hofmann did not publish the respective name form ‘*Listero-Piceetum*'; nevertheless, Pignatti published the name invalidly (Art. 3a).

Later, PIGNATTI & PIGNATTI (2014: 191) again published ‘*Listero-Piceetum* Mayer et Hofmann 1969', this time as an accepted name, albeit invalidly as well (Art. 3i, 39b).

These three names do not represent a syntaxonomical synonym of *Listero cordatae-Piceetum abietis* (Samek et al. 1957) P. Kučera 2022, because they represent phytochorologically different alpine Norway spruce community of non-extreme habitat, partially also *Lophozio-Piceetum* (p. p. min.).

*Syntaxonomical note.* – *Listero cordatae-Piceetum abietis* (Samek et al. 1957) P. Kučera 2022 belongs ecologically and floristically to the group (series) of distinctive natural acid Norway

spruce communities developed on soil ecologically specific scree habitats found hitherto in the Central European mountain ranges: *Betulo carpatica-Piceetum* Stöcker 1967 (ecologically the most unfavourable unit) – *Anastrepto-Piceetum* Stöcker 1967 – *Listero cordatae-Piceetum* – *Dryopterido dilatatae-Piceetum* Sýkora ex Jirásek 1996 (± the least extreme unit) (cf. STÖCKER 1967, 1968; SÝKORA 1971; JIRÁSEK 1996).

## 2.7. *Sphagno capillifolii-Piceetum abietis* Zukrigl 1973 nom. corr.

Nomenclatural type: ZUKRIGL (1973), tab 6, rel. 2, lectotype (WILLNER & ZUKRIGL 1999: 154).

Original name: *Sphagno-Piceetum* Zukrigl 1973 (ZUKRIGL 1973: 151), i.e. *Sphagno acutifolii-Piceetum abietis* Zukrigl 1973 nom. inept. (Rec. 10C, Art. 44) in the sense of lectotypification by WILLNER & ZUKRIGL (1999: 154) as well as their statement on *Sphagnum* species (cf. nomenclatural note 1 below).

Non: *Sphagno [quinquefarii]-Piceetum* (Tx. 1937) Hartmann 1953 (Rec. 10C, cf. KUČERA 2019b) [= *Piceetum excelsae sphagnetosum [quinquefarii]* Tx. 1937],

*Sphagno-Piceetum* auct. non (Tüxen 1937) Hartmann 1953 (e.g. HARTMANN 1953; SOFRON 1981), *Sphagno-Piceetum* Kuoch 1954 nom. superfl. (Art. 25, 29c), *Sphagno-Piceetum* Ellenberg et Klötzli 1974 nom. superfl. (Art. 25, 29c);

*Sphagno-Piceetum montanum* Stefanović et Popović 1961 nom. nud. (Art. 2b), *Sphagno-Piceetum montanum* Stefanović 1964 nom. inval. (Art. 3b);

*Sphagno girgensohnii-Piceetum* Polakowski 1962 nom. cons. propos. (cf. KUČERA 2019b), *Sphagno palustris-Piceetum* Šomšák 1979, *Sphagno acutifolii-Piceetum* (Březina et Hadač in Hadač et al. 1969) Hadač 1987 nom. illeg. (Art. 31).

Set of the diagnostic species within the evaluated dataset:

E<sub>j</sub>: *Carex canescens*, *Nardus stricta*, *Juncus filiformis*, *Eriophorum vaginatum*, *Carex echinata*, *Carex nigra*, \**Athyrium distentifolium*,

E<sub>o</sub>: *Polytrichum commune*, *Barbilophozia floerkei*, *Sphagnum rubellum*, *Pohlia nutans*, *Lophocolea heterophylla*, *Dicranum montanum*, \**Sphagnum capillifolium*.

Relevé data: KUČERA (2005): 65, rel. 3; KUČERA (2012a): 292, rel. 20 + page 295, rel. 30 + page 311, rel. 74 + page 312, rel. 77, + page 317, rel. 97. See Fig. 3.

This association constitutes a marginal community within the group of natural acid Norway spruce communities (*Piceion excelsae* Pawłowski ex Pawłowski et al. 1928), developed within the Western Carpathian region on bogside ecotones or groundwater-influenced habitats confined to gentle (moderate) slopes adjacent to mountain plateaus of some mountain ranges, mostly in the supramontane vegetation zone. The phytocoenoses are characterized by the co-occurrence of (1) mire species as *Eriophorum vaginatum*, *Carex echinata* etc. and selected *Sphagnum* species other than *S. girgensohnii* and (2) constantly present species characteristic of climax supramontane *Picea* woodland on acid soils (see below; KUČERA 2019b).

Canopy species composition in the hitherto known relevés from the Western Carpathians consists of the dominating *Picea abies*, frequently with cover lower than 50%, and admixed *Sorbus aucuparia* (ssp. *glabrata*). Occasionally *Abies alba* was present in tree form (KUČERA 2012: 80).

*Pinus mugo* is present in the understorey in several documented habitats of this community.

The field layer is dominated by *Vaccinium myrtillus*, higher cover is reached in some sites by constant species as *Calamagrostis villosa*, *Athyrium distentifolium* or, eventually, *Avenella flexuosa*.

Other constant companions are *Homogyne alpina* and *Dryopteris dilatata* (in some localities *D. expansa* is present as well). The characteristic floristic feature of *Sphagno capillifolii-Piceetum* phytocoenoses is the presence of habitat-specific sedges (*Carex canescens*, *C. nigra*, *C. echinata*), *Eriophorum vaginatum*, *Juncus filiformis* and, eventually, *Nardus stricta*. Current abundance of the latter species may reflect long-term impact of (former) high mountain grazing and associated (pre-)historical deforestation. In some documented phytocoenoses *Vaccinium vitis-idaea*, *Luzula sylvatica* ssp. *sylvatica*, rarely *Oxalis acetosella*, *L. luzuloides* and *Equisetum sylvaticum* are present. *Vaccinium uliginosum* was an indigenous species in some areas.

The ground layer has high cover within the phytocoenoses, about 60–80% in the relevé plots, and it is characterized by constant presence and dominance of two *Polytrichum* species (*P. formosum*, *P. commune*, occasionally only one of them) and peat mosses – especially *Sphagnum capillifolium*. *S. girgensohnii*, *S. rubellum* and *S. fuscum* were documented as well. *Dicranum scoparium* is constantly present, lower frequency have species *Plagiothecium curvifolium*, *D. montanum* and *Pleurozium schreberi*. *Calypogeia azurea*, *Lophocolea heterophylla*, *Pohlia nutans*, *Rhytidadelphus triquetrus* and other species were also recorded.

Sample phytocoenosis (KUČERA 2012a: 312, rel. 77, the Vaterné hole Mts, 1470 m a.s.l.):

E<sub>3</sub>: *Picea abies* 3, *Sorbus aucuparia* 1,

E<sub>2</sub>: *Pinus mugo* 2b, *P. abies* 1,

E<sub>1</sub>: *P. mugo* 1, *P. abies* +, *Sorbus aucuparia* +, *Abies alba* r, *Vaccinium myrtillus* 4, *Avenella flexuosa* 2a, *V. vitis-idaea* 2a, *Eriophorum vaginatum* 1, *Homogyne alpina* 1, *Lycopodium annotinum* 1, *Athyrium distentifolium* +, *Calamagrostis villosa* +, *Carex canescens* +, *Dryopteris dilatata* +, *Juncus filiformis* +,

E<sub>0</sub>: *Sphagnum capillifolium* 3, *Polytrichum formosum* 3, *Dicranum scoparium* 2a, *P. alpinum* 1, *P. commune* 1, *Sphagnum rubellum* 1, *Barbilophozia attenuata* +, *Barbilophozia lycopodioides* +, *Dicranum montanum* +, *Sphagnum girgensohnii* +, *Calypogeia integriflora* +.

The overall distribution of *Sphagno capillifolii-Piceetum* Zukrigl 1973 within Central Europe is insufficiently known. KUČERA (2019b) summarized published occurrences from the Western Carpathians,<sup>15</sup> in this phytocoenological statistic synthesis two other (phytocoenotically marginal) relevés from the Veľká Fatra Mts were included into the association. Similar, very rare stands were noticed in the Oravské Beskydy Mts. and Stolické vrchy Mts. (Kučera, ined.).

The equivalent habitats and phytocoenoses most probably also occur in the Czech Republic; however, CHYTRÝ et al. (2013b) included the relevant *Sphagnum*-rich communities inadequately into the association *Vaccinio uliginosi-Piceetum* Schubert 1972. EXNER's (2007) delimitation of the association *Sphagno capillifolii-Piceetum* Zukrigl 1973 from Austria should be re-evaluated as well.

*Nomenclatural note 1.* – Several authors published association names using the combination of genera names ‘*Sphagno-Piceetum*’ (cf. WILLNER & ZUKRIGL 1999; KUČERA 2012a; CHYTRÝ et al. 2013b). However, they are only fictitious homonyms in many cases, and usually they are not syntaxonomical synonyms (cf. Kučera 2019b).

To support the easier differentiation of the respective communities as well as scientific conservation of the well-established and phytocoenologically useful names (especially *Sphagno*

<sup>15</sup> Two relevés (KUČERA 2012a: 311–312, rels. 75, 76) were excluded from the here evaluated dataset due to methodical restrictions regarding the plot size (see chapter ‘Material and methods’).

*girgensohnii-Piceetum* Polakowski 1962, *Sphagno-Piceetum* Zukrigl 1973<sup>16)</sup>, KUČERA (2019b) published nomenclatural proposals to the completion of some names (cf. THEURILLAT et al. 2021, Rec. 10B, 10C); syntaxonomical reconsideration of the original diagnoses of the relevant units was resolved as well.

The original table of *Sphagno-Piceetum* Zukrigl 1973 published by ZUKRIGL (1973: 152) comprises four distinct phytocoenological communities (KUČERA 2019b, Suppl. A3: e7). As the nomenclatural type of this association (WILLNER & ZUKRIGL 1999: 154) is the only relevé representing one of these four units and at the same time containing only one *Sphagnum* species (ut *Sphagnum* cf. *capillifolium* by Zukrigl [1973], ut *S. capillifolium* by WILLNER & ZUKRIGL [1999: 154]), the association name could be completed to the form *Sphagno acutifolii-Piceetum* Zukrigl 1973 nom. inept., i.e. *Sphagno capillifolii-Piceetum* Zukrigl 1973 nom. corr. (KUČERA 2019b; cf. THEURILLAT et al. 2021).

*Nomenclatural note 2.* – On condition that the completion of the name *Sphagno-Piceetum* Zukrigl 1973 to the form *Sphagno capillifolii-Piceetum* Zukrigl 1973 nom. corr. (*Sphagno acutifolii-Piceetum* Zukrigl 1973 nom. inept) is accepted, *Sphagno acutifolii-Piceetum* (Březina et Hadač in Hadač et al. 1969) Hadač 1987 becomes a later homonym. As the latter unit represents an anthropogenically changed forest community correctly classified within the alliance *Luzulo-Fagion* Lohmeyer et Tx. in Tx. 1954 (KUČERA 2009b, 2012a: 250), the following name substitution is proposed here:

*Sphagno acutifolii-Abietetum* (Hadač 1987) P. Kučera 2022 nom. nov. *hoc loco*

Replaced name: *Sphagno acutifolii-Piceetum* (Březina et Hadač in Hadač et al. 1969) Hadač 1987 (HADAČ 1987: 13).

*Syntaxonomical note 1.* – Syntaxonomical interpretation of *Sphagno capillifolii-Piceetum* Zukrigl 1973 should strictly follow the lectotypification of this unit by WILLNER & ZUKRIGL (1999) as a transitional unit between the alliance *Piceion excelsae* Pawłowski ex Pawłowski et al. 1928 (however, within this alliance) and non-forest communities of the class *Oxycocco-Sphagnetea* Br.-Bl. et Tx. ex Westhof et al. 1964 or, eventually, even woodland (or krummholz-forest) bog communities of the class *Vaccinio uliginosi-Pinetea sylvestris* Passarge 1968 (cf. KUČERA 2019b).

*Syntaxonomical note 2.* – More abundant field data are required and a specialized study should be devoted to the more exact delimitation of *Sphagno capillifolii-Piceetum* Zukrigl 1973 vs. *Lophozio-Piceetum polytrichetosum communis* P. Kučera 2023 or, eventually, subunits of the association *Soldanello montanae-Piceetum* Volk in Br.-Bl. et al. 1939 (CHYTRÝ et al. 2013b; KUČERA 2019b) – including the subassociation *Soldanello montanae-Piceetum molinietosum caeruleae* (Sýkora ex Jirásek 1996) P. Kučera 2023 comb. nov. *hoc loco* (basionym: *Sphagno-Piceetum molinietosum* Sýkora ex Jirásek 1996 (JIRÁSEK 1996: 250); nomenclatural type: SÝKORA (1971), tab. 6, rel. 8, holotype (JIRÁSEK 1996: 250); incl. *Molinio-Piceetum* Sýkora 1971 nom. inval. (Art. 3b); differential taxa: *Molinia caerulea*, (?) *Trientalis europaea*) (cf. KUČERA in red.).

## 2.8. Notes on the delimitation of the association *Dryopterido dilatatae-Piceetum abietis* Sýkora ex Jirásek 1996 and its occurrence in the Western Carpathians

Nomenclatural syn.: *Dryopterido dilatatae-Piceetum* Sýkora 1971 nom. inval. (Art. 3b, 14), *Dryopterido dilatatae-Piceetum* Sýkora ex Sofron 1981 nom. inval. (Art. 30, 5)

<sup>16</sup> See above the note under the paragraph ‘Original name’.

The original delimitation of this association consists of four relevés of the Norway spruce phytocoenoses found in the Jizerské Hory Mts, Czech Republic, on steep ([20]45–50°) to the north and east oriented bouldery slopes, with habitat type similar to the lower-elevated communities of the alliance *Tilio-Acerion* Klika 1955 (SÝKORA 1971: 45). *Picea abies* is the dominating tree.

The community is poor in species, characterized by the constant presence of *Sorbus aucuparia* in the canopy (in the understorey too) as well as by the co-dominant species *Dryopteris dilatata* and *Vaccinium myrtillus*. Accompanying species are *Vaccinium vitis-idaea*, *Rubus idaea* and *Trientalis europaea*; the rich abundance of the latter species probably reflects the phytochorological position of the Hercynian mountain ranges within Central Europe. In a lower number of relevés *Lycopodium annotinum* (rarely also *Huperzia selago*), *Calamagrostis villosa* were recorded, in one from four relevés, for example, *Avenella flexuosa*, *Oxalis acetosella* and *Homogyne alpina*. The absence of *Athyrium distentifolium* is noteworthy.

Characteristic feature of the ground layer is the explicit domination of *Polytrichum formosum*, accompanied by *Sphagnum girgensohnii* (occasionally *S. capillifolium*), *Dicranum scoparium* is frequent as well.

The mostly negative floristic differentiation of the *Dryopterido dilatatae-Piceetum* phytocoenoses (sensu SÝKORA 1971!), especially against the other species-poor phytocoenoses of the association *Lophozio-Piceetum*, is the reason that they are frequently classified into the '*Calamagrostio villosae-Piceetum*'-type of communities (cf. JIRÁSEK 1996, 2002 vs. EXNER 2007; CHYTRÝ et al. 2013b). However, *Dryopterido dilatatae-Piceetum* is ecologically more closely related to the association *Listero cordatae-Piceetum* (see above) – the differences are more favourable soil conditions of the former unit as well as distinct floristic patterns of these two associations.

Stands of this community from Slovakia were referred by SOFRON (1976 msc., 1981: 48) from the northern part of the High Tatras. The evaluation of naturalness of the respective phytocoenoses should be subject of further detailed studies, as *Acer pseudoplatanus* might also be a potential natural component of the stands (cf. MYCZKOVSKI & LESÍNSKI 1974) and *Fagus sylvatica* absence in the area of Baboš Mt. is the result of past land management – in the adjacent region remnants of *Fagus* populations are present (cf. SOFRON 1976 vs. SAMEK et al. 1957; KANKA 2008).

*Nomenclatural note.* – The name *Dryopterido dilatatae-Piceetum* Sýkora ex Sofron 1981 is usually accepted as valid form of this association name (see JIRÁSEK 1996, 2002; CHYTRÝ et al. 2013b); however, the name was not validly published by SOFRON (1981) (see KUČERA 2012a).

*Syntaxonomical note.* – Although SOFRON (1981: 48) classified his own phytocoenological relevé from the Ore Mountains (the Krušné Hory Mts) into the *Dryopterido dilatatae-Piceetum*, the documented community does not correspond to the referred association neither ecologically (wet peaty soil) nor floristically (*Carex canescens!*) (KUČERA 2012a): the more adequate classification is within the association *Soldanello montanae-Piceetum abietis* Volk in Br.-Bl. et al. 1939 nom. corr.

The extent of the *Dryopterido dilatatae-Piceetum* distribution in the Czech Republic indicated by JIRÁSEK (1996, 2002) should be verified: for example, the record from the Moravian-Silesian Beskids represents a historical anthropogenically changed stand replacing the former natural upper montane mixed woodland with *Fagus* of the class *Carpino-Fagetea* (KUČERA 2012a). The phytocoenological classification of the rest of *Dryopterido dilatatae-Piceetum* records of Jirásek (1996) as communities of the class *Vaccinio-Piceetea* should be re-evaluated as well.

Similarly, SOLOMAKHA et al. (2004, tab. 3.27) included into the association *Dryopterido dilatatae-Piceetum* phytocoenoses which could not be syntaxonomically identified with this association and do not belong to the class *Vaccinio-Piceetea*: their correct classification is within the order *Luzulo-Fagetalia sylvaticae* Scamoni et Passarge 1959.

### 3. Higher syntaxonomical units of acid Norway spruce woodlands

*Picea abies* communities were traditionally classified syntaxonomically within the order *Piceetalia abietis* Pawłowski ex Pawłowski et al. 1928 and the alliance *Piceion abietis* Pawłowski ex Pawłowski et al. 1928 which originally documented non-carbonate Norway spruce (and Arolla pine) communities (PAWŁOWSKI 1928; and subsequently PAWŁOWSKI et al. 1928) or, alternatively, they were usually included under younger synonymous names *Vaccinio-Piceetalia* Br.-Bl. in Br.-Bl. et al. 1939 and *Vaccinio-Piceion* Br.-Bl. in Br.-Bl. et al. 1939 (BRAUN-BLANQUET et al. 1939; TÜXEN 1955; OBERDORFER 1957; OBERDORFER et al. 1967; MATUSZKIEWICZ 1977).

However, already HADAČ (1962; in HADAČ et al. 1969) recognized distinct ecological and floristical uniqueness of calcicolous Norway spruce woodlands and described for them a separate syntaxonomical unit in the rank of an order – *Athyrio-Piceetalia* – the acceptance of which is continuously growing among European scientists (cf. the literature overview as well as important nomenclatural proposal to a name change to *Cortuso-Piceetalia* by KUČERA 2023). The respective plant communities are (usually) rich in calcicoles (*Asplenium viride*, *Calamagrostis varia*, *Corthusa matthioli*, *Sesleria albicans* etc.) as well as rich in species which (with few exceptions) prefer calcareous soils within the supramontane altitudinal vegetation zone of Central European mountain ranges (*Astrantia major*, *Galium schultesii*, *Geranium sylvaticum*, *Phyteuma spicatum*, *Polygonatum verticillatum*, *Primula elatior*, *Valeriana tripteris*) (HADAČ et al. 1969; KUČERA 2012a, 2022; JUVAN et al. 2013).

Nevertheless, as a result of long-term traditional use – based on a too broad original description of the class by BRAUN-BLANQUET et al. (1939) and the traditional focus on siliciculous Norway spruce communities even in later trend-setting surveys (OBERDORFER 1957; SEIBERT 1992; CHYTRÝ et al. 2013b), the whole class *Vaccinio-Piceetea* Br.-Bl. in Br.-Bl. et al. 1939 used to be commonly characterized as a unit of acidophilic communities, of forests on acid, base-poor, oligotrophic soils, or the species composition of its plant communities is characterized by acidophytes/calcifuges (see SEIBERT 1992; THEURILLAT et al. 1995; RAMEAU 1997; JIRÁSEK 2002; BARDAT et al. 2004; RIVAS-MARTÍNEZ et al. 2011; ERMAKOV 2012; ŠILC & ČARNI 2012; CHYTRÝ et al. 2013b; BIONDI et al. 2014; MUCINA et al. 2016; DUBYNA et al. 2019; BERGMEIER 2020).

These descriptions are inappropriate if all communities of the class *Vaccinio-Piceetea* need to be addressed as one vegetation type, i.e. including various calcareous *Picea abies* and *Pinus cembra* woodland types of the Carpathians and the Alps. This is also the reason why the class *Vaccinio-Piceetea* as such could not be geobotanically characterized by ecological epithets, which would imply a calcifugous species composition of the included plant communities (see the contradiction in the ecological descriptions of the class and the subordinated order *Athyrio-Piceetalia* by MUCINA et al. 2016; BERGMEIER 2020).

Instead of species including *Vaccinium myrtillus*, *V. vitis-idaea*, *Avenella flexuosa*, *Melampyrum sylvaticum*, *Lycopodium annotinum*, *Trientalis europaea*, *Oxalis acetosella* or *Dicranum scoparium* and *Pleurozium schreberi* (BRAUN-BLANQUET et al. 1939; WALLNÖFER 1993; EXNER 2007; CHYTRÝ

et al. 2013b; CHIFU 2014; DUBYNA et al. 2019 etc.) which are not ecologically and chorologically restricted to *Picea abies* communities<sup>17</sup> and frequent in a broad variety of non-forest vegetation types,<sup>18</sup> the class *Vaccinio-Piceetea* Br.-Bl. in Br.-Bl. et al. 1939 should be syntaxonomically qualified by species which are in general common for both calcicolous and silicolous communities of natural Norway spruce (and Arolla pine) phytocoenoses and distinguishing them as an entity within the respective basic formation type (cf. THEURILLAT et al. 1995), including *Adenostyles alliariae*, *Calamagrostis villosa*, *Gentiana asclepiadea*, *Homogyne alpina*, *Luzula sylvatica* (see Table 1 and: JIRÁSEK 1996; WILLNER et al. 2007, tab. 39 and 33; KUČERA 2012a, 2017, 2019b tab. 1, 2022, in red., tables 1–3; CHYTRÝ et al. 2013b; COLDEA 2015), bearing in mind their partial overlapping into upper montane *Carpino-Fagetea* woodlands.

*Syntaxonomical note.* – Species including (group A) *Athyrium filix-femina*, *Carex digitata*, *Fragaria vesca*, *Gymnocarpium dryopteris*, *Maianthemum bifolium*, *Luzula pilosa*, *Oxalis acetosella*, *Trientalis europaea*; *Dicranum scoparium*, *Hylocomium splendens*, *Pleurozium schreberi*, *Rhytidiodelphus triquetrus*, *Vaccinium myrtillus* or (group B) *Betula pubescens*, *Empetrum nigrum*, *Pinus sylvestris*, *Populus tremula* are in the studies and surveys on Siberian and in particular on European Russian woodland vegetation referred to as diagnostic species of the alliance *Piceion abietis* (or *Piceetalia abietis/Vaccinio-Piceetea*) (ERMAKOV et al. 2002; MARTYNENKO et al. 2008; ZAUGOLNOVA et al. 2009; ERMAKOV & MAKHATKOV 2011; ERMAKOV 2013, 2014; LASHCHINSKY & PISARENKO 2016; MOROZOVA et al. 2017; BRIANSKAIA et al. 2019).

However, the statistical results of the surveys cited above from Austria, Czech Republic, Germany, Slovakia justify the assessment that these species are not specific for the alliance *Piceion abietis* (see group A above) or they are not regular natural components of its communities in Central Europe (see group B) (EXNER 2007; KUČERA 2012a, 2019b; CHYTRÝ et al. 2013b) – the region where this unit was originally described. This is even more true for species selected as diagnostic in the mentioned Russian studies which are not native in the respective area of Central Europe or relevant adjacent regions (western Alps and Pyrenees to Southern Carpathians), e.g. <sup>†</sup>*Abies sibirica*, <sup>†</sup>*Larix sibirica*, <sup>†</sup>*Lonicera caerulea* ssp. *altaica*, <sup>†</sup>*Picea obovata* or even within Europe – <sup>†</sup>*Pyrola asarifolia* ssp. *incarnata*, <sup>†</sup>*Rhododendron dauricum* (marginally <sup>†</sup>*Orthilia obtusata*).

Moreover, the referred Northeast European and Siberian coniferous woodlands (various taiga vegetation types) are characterized by the absence of the species which are – within the woodland types formation (THEURILLAT et al. 1995) – typical of the communities of the class *Vaccinio-Piceetea* in the European orobomes of the Alps, Carpathians etc. (see above).

Therefore, similar to the example of exclusion of the order *Abietetalia sibiricae* (Ermakov in Ermakov et al. 2000) Ermakov 2006 from the class *Carpino-Fagetea* into a separate syntaxonomical class *Asaro europaei-Abietetea sibiricae* Ermakov et al. in Willner et al. 2016 (WILLNER et al. 2016), the considered Northeast European (to Siberian) coniferous woodland communities

<sup>17</sup> For the Central European woodland vegetation see for example: HÖLZEL et al. (1996); MATUSZKIEWICZ (2002); WILLNER et al. (2007); HEINKEN (2008); CHYTRÝ et al. (2013a); SLEZÁK et al. (2014, 2016, 2020); UJHÁZYOVÁ et al. (2021).

<sup>18</sup> See for example CHYTRÝ & TICHÝ (2003); JAROLÍMEK et al. (2008a) [however, considered should be the respective too wide syntaxonomical delimitations of the class *Vaccinio-Piceetea*, cf. THEURILLAT et al. (1995) and ŠIBÍK (2007) for the first survey and KUČERA (2012a, 2022 and this study) for the second one] as well as HÁJEK & HÁBEROVÁ (2001); ŠOLTÉS et al. (2001); CHYTRÝ et al. (2007); KLIMENT et al. (2007); ŠIBÍK et al. (2010); HÁJKOVÁ et al. (2011); KLIMENT & UJHÁZY (2014).

usually classified within the alliance *Piceion abietis* are here delimited into a separate class *Piceo obovatae-Abietetea sibiricae* and the following syntaxonomical system is proposed:<sup>19</sup>

### Class *Piceo obovatae-Abietetea sibiricae* P. Kučera cl. nov. hoc loco

Nomenclatural type: *Calamagrostio arundinaceae-Abietetalia sibiricae* P. Kučera ord. nov. (see below)

Original diagnosis: *Clematido sibiricae-Abietetalia sibiricae* P. Kučera ord. nov., *Calamagrostio arundinaceae- Abietetalia sibiricae* P. Kučera ord. nov., *Vaccinio vitis-idaeae-Piceetalia obovatae* P. Kučera ord. nov.

Non: *Asaro europaei-Abietetea sibiricae* Ermakov et al. in Willner et al. 2016, *Dicrano-Pinetea* Hartmann et Jahn 1967, *Vaccinio-Piceetea* Br.-Bl. in Br.-Bl. et al. 1939, *Vaccinio uliginosi-Pinetea* Passarge 1968

Differential species: <sup>†</sup>*Clematis sibirica*, *Linnaea borealis*, *Luzula pilosa*, *Melica nutans*, *Trientalis europaea*; <sup>†</sup>*Abies sibirica*, *Betula pubescens*, <sup>†</sup>*Picea obovata*, <sup>†</sup>*Pinus sibirica*, *Pinus sylvestris* (against the class *Vaccinio-Piceetea* Br.-Bl. in Br.-Bl. et al. 1939); negatively differentiated against *Asaro europaei-Abietetea sibiricae* Ermakov et al. in Willner et al. 2016 by the absence of South to East Siberian species.

#### A. Very species-rich mesotrophic (to eutrophic) order *Clematido sibiricae-Abietetalia sibiricae* P. Kučera ord. nov. hoc loco

Nomenclatural type: <sup>†</sup>*Clematido sibiricae-Piceion obovatae* (Zaugolnova et al. 2009) P. Kučera stat. nov. (see below)

Original diagnosis: <sup>†</sup>*Clematido sibiricae-Piceion obovatae* (Zaugolnova et al. 2009) P. Kučera stat. nov. (see below), *Aconito septentrionalis-Piceion obovatae* Solomeshch et al. in Martynenko et al. 2008

Non: *Abietetalia sibiricae* (Ermakov in Ermakov et al. 2000) Ermakov 2006, *Piceo obovatae-Pinetalia sibiricae* Ermakov 2013<sup>20</sup>

Differential species: <sup>†</sup>*Aconitum septentrionale*, *Aegopodium podagraria*, *Cirsium heterophyllum*, <sup>†</sup>*Clematis sibirica*, *Fragaria vesca*, *Lathyrus vernus*, *Lonicera xylosteum*, <sup>†</sup>*Parasenecio hastatus*, *Paris quadrifolia*, *Pulmonaria mollis*, *P. obscura*, *Stellaria nemorum*.

##### A.1. Alliance *Aconito septentrionalis-Piceion obovatae* Solomeshch et al. in Martynenko et al. 2008

Differential species against the alliance *Clematido sibiricae-Piceion obovatae*: *Acer platanoides*, *Carex pilosa*, *Quercus robur*, *Tilia cordata*, *Ulmus glabra*.

Including the association: *Clematido sibiricae-Piceetum abietis* (Zaugolnova et Morozova in Morozova et al. 2017) P. Kučera stat. nov. hoc loco: basionym – *Rhodobryo rosei-Piceetum abietis abietetosum sibiricae* Zaugolnova et Morozova in Morozova et al. 2017 (MOROZOVA et al. 2017: 48); nomenclatural type: MOROZOVA et al. (2017: 48).

Note: The nomenclatural type of the alliance – the association *Cerastio pauciflori-Piceetum obovatae* Solomesch et al. in Martynenko et al. 2008 (MARTYNENKO et al. 2008) as well the same Eastern European geobotanical and geographical position with the alliance *Clematido sibiricae-Piceion obovatae* present stronger phytocoenological ties than the similarity of *Aconito septentrionalis-Piceion obovatae* with the alliance *Milio effusi-Abietion sibiricae* Zhitlukhina ex Ermakov et al. 2000 (order *Abietetalia sibiricae* (Ermakov in Ermakov et al. 2000) Ermakov 2006, class *Asaro europaei-Abietetea sibiricae* Ermakov et al. in Willner et al. 2016) described from mountain ranges of South Siberia.

<sup>19</sup> Only the most essential data of subordinated units are given.

<sup>20</sup> Both orders belong to the geobotanical region of high South Siberian mountain ranges. Their subordinated alliances (including *Aconito rubicundi-Abietion sibiricae* Anenkhonov et Chytrý 1998) should be probably united into one order not belonging to the class *Piceo obovatae-Abietetea sibiricae*.

**A.2. Alliance *Clematido sibiricae-Piceion obovatae* (Zaugolnova et al. 2009) P. Kučera stat. nov. hoc loco et nom. corr.**

Basionym: *Atrageno sibiricae-Piceenion obovatae* Zaugolnova et al. 2009 (ZAUGOLNOVA et al. 2009: 5, 8). See also: ALEINIKOV et al. (2016), SHEVCHENKO & SMIRNOVA (2017).

**B. Submesotrophic order *Calamagrostio arundinaceae-Abietetalia sibiricae* P. Kučera ord. nov. hoc loco**

Nomenclatural type: *Melico nutantis-Abietion sibiricae* P. Kučera all. nov. (see below)

Original diagnosis: *Melico nutantis-Abietion sibiricae* P. Kučera all. nov. (see below)

Differential species: *Calamagrostis arundinacea*, *Linnaea borealis*, *Maianthemum bifolium*, *Trientalis europaea* (largely negative species differentiation, similarly as in case of the order *Piceetalia abietis* within the class *Vaccinio-Piceetea*: see KUČERA 2019b – tab. 1; KUČERA in red. – tab. 1); <sup>†</sup>*Abies sibirica*, *Athyrium filix-femina*, *Carex digitata*, *Melica nutans*, *Stellaria holostea* ([lower constant] differential species against the order *Vaccinio vitis-idaeae-Piceetalia obovatae*)

**B.1. Alliance *Melico nutantis-Abietion sibiricae* P. Kučera all. nov. hoc loco**

Nomenclatural type: *Melico nutantis-Abietetum sibiricae* (Martynenko et al. ex P. Kučera 2023) P. Kučera stat. nov. (see below).

Original diagnosis: *Melico nutantis-Abietetum sibiricae* (Martynenko et al. ex P. Kučera 2023) P. Kučera stat. nov. (see below).

Differential species: *Hieracium albocostatum*, <sup>†</sup>*Hieracium subpellucidum*, *Linnaea borealis*, *Gymnocarpium dryopteris*, *Oxalis acetosella*, *Phegopteris connectilis*, *Trientalis europaea* (largely negative species differentiation, similar as in case of the alliance *Piceion abietis* within the class *Vaccinio-Piceetea*: see KUČERA in red. – tab. 1, tab. 4).

**B.1.1. Association *Melico nutantis-Abietetum sibiricae* (Martynenko et al. ex P. Kučera 2023) P. Kučera stat. nov. hoc loco**

Nomenclatural type: MARTYNNENKO et al. (2008), tab. 73, rel. 13.

Original diagnosis: MARTYNNENKO et al. (2008), tab. 73, rels. 1–33.

Basionym of *Melico nutantis-Abietetum sibiricae* (Martynenko et al. ex P. Kučera 2023) P. Kučera 2023: *Linnaeo borealis-Piceetum abietetosum sibiricae* Martynenko et al. ex P. Kučera subass. nov. hoc loco [ $\equiv$  *Linnaeo borealis-Piceetum abietetosum sibiricae* Martynenko et al. 2008 nom. inval. (Art. 3b, 3e); MARTYNNENKO et al. (2008: 232, 439, 444)]; nomenclatural type: MARTYNNENKO et al. (2008), tab. 73, rel. 13, holotypus hoc loco (i.e. following the proposal of MARTYNNENKO et al. 2008).

**C. Oligotrophic order *Vaccinio vitis-idaeae-Piceetalia obovatae* P. Kučera ord. nov. hoc loco**

Nomenclatural type: *Vaccinio vitis-idaeae-Piceion obovatae* P. Kučera all. nov. (see below)

Original diagnosis: *Vaccinio vitis-idaeae-Piceion obovatae* P. Kučera all. nov. (see below), *Empetrio-Piceion obovatae* Morozova in Morozova et al. 2008

Differential species: *Avenella flexuosa*, <sup>†</sup>*Cornus suecica*, *Empetrum hermaphroditum*, *Juniperus sibirica*, *Pinus sylvestris* (tree layer), *Vaccinium uliginosum* (? *V. gaultherioides*); *Cladonia stellaris*

**C.1. Alliance *Vaccinio vitis-idaeae-Piceion obovatae* P. Kučera all. nov. hoc loco**

Nomenclatural type: *Vaccinio vitis-idaeae-Piceetum obovatae* P. Kučera ass. nov. (see below)

Original diagnosis: *Vaccinio vitis-idaeae-Piceetum obovatae* P. Kučera ass. nov. (see below)

Differential species: <sup>†</sup>*Abies sibirica*, *Maianthemum bifolium*, *Vaccinium vitis-idaea* (dom.); *Dicranum montanum*, *Ptilium crista-castrensis*

Non: *Pino sibiricae-Laricion sibiricae* Guinochet ex Dostálek et al. 1988<sup>21</sup>

C.1.1. Association *Vaccinio vitis-idaeae-Piceetum obovatae* P. Kučera ass. nov. hoc loco

Nomenclatural type: MARTYNENKO et al. (2008), tab. 72, rel. 14.

Original diagnosis: MARTYNENKO et al. (2008), tab. 72, rels. 11–14.

## C.2. Alliance *Empetrio-Piceion obovatae* Morozova et al. 2008<sup>22</sup>

C.2.1. Including the association: *Junipero sibiricae-Piceetum obovatae* P. Kučera ass. nov. hoc loco

Nomenclatural type: MOROZOVA et al. (2008), tab. 6, rel. 6 (26), holotypus hoc loco

Incl.: *Flavocetrario nivalis-Pinetum sylvestris typicum* var. *Picea obovata* – MOROZOVA et al. (2008)

This association ecologically represents a marginal unit of the class *Abieteto sibiricae-Piceetea obovatae*, transitional towards *Pinus sylvestris* taiga woodland (cf. *Dicrano-Pinetea* Hartmann et Jahn 1967).

C.2.2. Including the community *Salix glauca-Picea obovata* Martynenko et al. 2008

## 3.1. *Piceetalia abietis* Pawłowski ex Pawłowski et al. 1928 nom. corr.<sup>23</sup>

Nomenclatural type: alliance *Piceion excelsae* Pawłowski ex Pawłowski et al. 1928 (Pawłowski et al. 1928: 257), automatic lectotype (Art. 20).

Original name: *Piceetalia excelsae* Pawłowski ex Pawłowski et al. 1928 nom. incept. (Art. 44)

Nomenc. syn.: *Myrtillo-Piceetalia excelsae* Hadač 1962 nom. superfl. (Art. 10, 14b, 29c)<sup>24</sup>

Syntax. syn.: *Vaccinio-Piceetalia* Br.-Bl. in Br.-Bl. et al. 1939 nom. illeg.<sup>25</sup>

Differential species (see KUČERA 2019b, Suppl. B1/Tab. 1): *Dryopteris dilatata*, *Avenella flexuosa*; *Polytrichum formosum*, *Lophozia ventricosa*, *Bazzania tricrenata*, *Calypogeia integriflora* (mostly negative to quantitative species differentiation against the order *Cortuso matthioli-Piceetalia*).

*Floristical delimitation.* – Communities of the order *Piceetalia abietis* constitute a parallel ecological group to the order *Cortuso matthioli-Piceetalia abietis* P. Kučera 2022. They develop on nutrient-poor and very poor soils inducing usually remarkable low abundance of species growing in the respective phytocoenoses. The essential tree species are *Picea abies* and *Sorbus aucuparia*, in the hochgebirge mountain ranges the canopy species composition is enriched by *Larix decidua* and *Pinus cembra*. Norway spruce is within the Pyrenees replaced by <sup>†</sup>*Pinus uncinata* which participates in *Vaccinio-Piceetea* communities also in the western Alps.

<sup>21</sup> The alliance as defined by its nomenclatural type (see DOSTÁLEK et al. 1988: 33; GUINOCHE 1982) does not belong to the class *Piceo obovatae-Abietetea sibiricae* due to its East Siberian geobotanical affiliation.

<sup>22</sup> Classification of this alliance within the order *Ledo palustris-Laricetalia gmelinii* Ermakov in Ermakov et Alsynbayev 2004 and the assigned short characteristics 'Northeastern European taiga on long-frozen soils and permafrost' by MUCINA et al. (2016) does not correspond to the unit delimitation by the original authors MOROZOVA et al. (2008).

<sup>23</sup> See the comment on the author's citation by KUČERA (2013b).

<sup>24</sup> The author's reference to original diagnosis of the subordinated name *Myrtillo-Piceion* Březina et Hadač in Hadač 1962 (indirectly) includes the nomenclatural type of the alliance *Piceion abietis* Pawłowski ex Pawłowski et al. 1928 nom. corr. (cf. KRAJINA 1933: 152).

<sup>25</sup> Following the regulations of the 3<sup>rd</sup> edition of the syntaxonomical Code (WEBER et al. 2000), this name was evaluated as nomen invalidum, therefore also the superordinated name *Vaccinio-Piceetea* Br.-Bl. in Br.-Bl. et al. 1939 had to be regarded as invalidly published (KUČERA 2010b; cf. Theurillat in WILLNER et al. 2015: 179).

The field layer species composition of the *Piceetalia abietis* communities is generally characterized in a negative way: by absence or only very low frequency of species typical of calcareous *Cortuso matthioli-Piceetalia abietis* P. Kučera 2022 and as well as of wetland woodlands of *Sphagno palustris-Piceetalia abietis* P. Kučera 2019 (KUČERA 2019b, suppl. B1/tab. 1, 2022, tab. 4, in red.).

With spatially adjacent but altitudinally lower lying montane mixed *Fagus sylvatica* woodlands of the same type of geological background, they have common occurrence of *Luzula sylvatica* ssp. *sylvatica*, *Gentiana asclepiadea*, *Adenostyles alliariae*, *Homogyne alpina*, *Athyrium distentifolium*, *Calamagrostis villosa*, etc. (majority of them also grow in calcareous montane and supramontane woodlands). The occurrence of species including *Avenella flexuosa*, *Dryopteris carthusiana* as well as *Vaccinium myrtillus*, *V. vitis-idaea*, *Luzula luzuloides* and *D. expansa* expresses ecological similarity of *Piceetalia abietis* communities to acid woodlands from other syntaxonomical classes. Furthermore, their species pool includes taxa common in woodlands in general, e.g. *Oxalis acetosella*, *Rubus idaeus*, *Dryopteris dilatata*, *Prenanthes purpurea*. In the region of the Tatras and the Low Tatras, *Soldanella marmarossiensis* agg. (cf. VALACHOVIČ et al. 2019) participates in the species composition.

Occurrence of slightly more nutrient-demanding species is concentrated only to some communities (such as *Solidagini virgaureae-Piceetum* or *Parido quadrifoliae-Piceetum*), for example, *Acetosa arifolia*, *Stellaria nemorum*, *Veratrum album* ssp. *lobelianum*, *Senecio nemorensis* agg., *Solidago virgaurea*, *Calamagrostis arundinacea*, *Athyrium filix femina*, *Cicerbita alpina* and *Doronicum austriacum*. Remarkable is the considerable difference in their distribution pattern within mittelgebirge vs. hochgebirge mountain ranges, as such species could be more or less absent in natural acid supramontane Norway spruce communities of the first group.

Moreover, in the *Piceetalia abietis* communities are only exceptionally and usually infrequently found species as *Milium effusum*, *Mycelis muralis*, *Viola biflora*, *Hieracium murorum*, *Paris quadrifolia*, *Valeriana tripteris*, *Phyteuma spicatum* etc. Their presence indicates uncommon habitats with especially favourable soil ecological conditions (high abundance of these species is typical for *Cortuso matthioli-Piceetalia* communities, cf. KUČERA 2022).

Following species are bound to ecologically specific habitats within the order *Piceetalia abietis*: *Empetrum hermaphroditum*, *Listera cordata*, *Huperzia selago*, *Lycopodium annotinum*, *Melampyrum sylvaticum* etc., species of hochgebirge mountain ranges *Gentiana punctata*, *Vaccinium gaultherioides*, *Ligusticum mutellina*, eventually also mire species (*Carex nigra*, *Eriophorum vaginatum*, within the association *Sphagno capillifolii-Piceetum*; KUČERA 2019b).

Bryophyte species composition of the *Piceetalia abietis* communities is characterized by the absence of calcicoles, in addition, calcifuges like *Lophozia ventricosa* and *Mylia taylori* are present in some communities. In general, common mosses predominate in the ground layer of the phytocoenoses, especially *Polytrichum formosum*, *Dicranum scoparium*, *Pleurozium schreberi*, *Plagiothecium curvifolium* etc. Some woodland types are characterized by abundant peat mosses, primarily *Sphagnum capillifolium* and *S. girgensohnii*. Lichens are growing in the phytocoenoses usually within more extreme habitat types only.

*Ecological delimitation.* – The ecological environment for the development of *Piceetalia abietis* communities is provided by soils with a low supply of available nutrients, with strongly acidic to extremely acidic soil pH (even below 4.0 value; cf. ŠOLTÉS 1976) and with low nitrification (HADÁČ

et al. 1969). Therefore, they are exclusively bound to non-carbonate geological background only – on granitoid rocks (granites, gneisses, tonalites etc.), quartzites, non-calcareous flysch and so on. The occupied soil types are podzols (cf. ŠÁLY 1986) and rankers (non-carbonate leptosols as haplic leptosols to leptic podzols), in habitats with more extreme relief, there are also lithosols (lithic leptosols). In the region of the Western Carpathians, presence of cambisol soil type under a Norway spruce stand usually indicates (sub-)anthropogenic origin of the current woodland on a former (ancient) *Carpino-Fagetea* habitat.

The *Piceetalia abietis* communities can grow on carbonate rocks only in the case of development of very thick isolating soil layer which prevents the existence and successful growth of calcicoles as well as more nutrient-demanding species. In flat relief habitats periodical waterlogging can occur here and there, in the vicinity of bogs, springs or on floodplains of mountain streams more permanent waterlogging.

*Syntaxonomical delimitation.* – Similar to *Cortuso matthioli-Piceetalia* classification (KUČERA 2022), the order *Piceetalia abietis* has to be syntaxonomically divided into four basic groups.

(A) The first of them is the alliance *Piceion abietis* Pawłowski ex Pawłowski et al. 1928 (see below) which includes communities of the supramontane Norway spruce woodlands in particular of Central to Southeastern Europe, covering the uppermost elevations of high mountain ranges which do not reach or only slightly exceed the natural alpine forest line (so-called mittelgebirge mountain ranges, cf. KUČERA 2022). Moreover, they form the lower part of the uppermost forest zone – natural coniferous woodland – of the European hochgebirge mountain ranges as the Alps and the Tatra Mountains.

(B) The alliance *Homogyno alpinae-Pinion cembrae* P. Kučera 2017 (syn. *Pinion cembrae* Rivas-Martínez in Rivas-Martínez et al. 2011 nom. inval.) represents an ecological and floristical analogy to calcicolous *Calamagrostio variae-Pinion cembrae* P. Kučera 2017 (cf. KUČERA 2017, KUČERA & BARANČOK 2021). Its communities comprising the Arolla pine and mixed Arolla pine woodlands shape the upper part of the coniferous zone of the mentioned hochgebirge mountain ranges which provided a postglacial (especially post-Boreal and post-Atlantic) refugium for *Pinus cembra* populations. Despite of its less expressed floristical differentiation from *Piceion abietis* (see Table 3, the Western Carpathian phytocoenoses are impoverished in species in comparison to the Alps or Southwestern Carpathians) than in the case of their calcicolous counterparts *Calamagrostio variae-Pinion cembrae* – *Cortuso matthioli-Piceion*, the alliance of acid (mixed) Arolla pine woodlands should be recognized as a separate syntaxon due to its specific ecology, distribution patterns and postglacial history. This view is supported also by the potential and advantageous practical use of the unit, for example in forest management and nature conservation.

(C) Geographically vicariant unit of the Pyrenees is the alliance *Pinion uncinatae* Rivas-Martínez et Costa 1998 (corresp. name *Rhododendro ferruginei-Pinenion uncinatae* Rivas-Martínez et al. 1991) which is incorrectly identified by various authors with the calcicolous alliance *Seslerio caeruleae-Pinion uncinatae* Vigo 1974 (cf. RIVAS-MARTÍNEZ & COSTA 1998; RIVAS-MARTÍNEZ et al. 2001; THÉBAUD & BERNARD 2018), because the latter unit syntaxonomically belongs to the order *Cortuso matthioli-Piceetalia* P. Kučera 2022. The *Pinion uncinatae* communities are predominated by <sup>†</sup>*Pinus uncinata* (and *Abies alba*) and they form a separate supramontane (to altimontane) altitudinal vegetation zone in that region.

Table 3. Differential table of the alliances of the order *Piceetalia abietis* Pawłowski ex Pawłowski et al. 1928 in Slovakia with values of constancy (%) and fidelity ( $\phi \times 100$ ) in the exponent.

The relevé dataset is identical with tab. 3 (synoptic table of the order *Piceetalia abietis*) compiled by KučERA (in red.). Field and ground layer species with frequency lower than 5% in an individual column are omitted.

Group 1 – *Piceion abietis* Pawłowski ex Pawłowski et al. 1928 nom. corr.

Group 2 – *Homogyno alpinae-Pinion cembrae* P. Kučera 2017

Group No.	1	2
No. of relevés	109	76
Tree and shrub species		
Canopy (E <sub>3</sub> )		
<i>Picea abies</i>	<b>98</b> –	<b>99</b> –
<i>Pinus cembra</i>	. –	<b>100</b> <sup>100.0</sup>
<i>Sorbus aucuparia</i>	25 –	37 –
<i>Larix decidua</i>	6 –	11 –
<i>Betula carpatica</i>	3 –	. –
<i>Salix silesiaca</i>	1 –	1 –
<i>Salix caprea</i>	1 –	. –
Understorey		
E <sub>2</sub>		
<i>Picea abies</i>	32 –	<b>51</b> <sup>19.5</sup>
<i>Pinus mugo</i>	9 –	46 <sup>41.2</sup>
<i>Sorbus aucuparia</i>	14 –	32 <sup>21.3</sup>
<i>Pinus cembra</i>	. –	21 <sup>34.3</sup>
<i>Salix silesiaca</i>	1 –	4 –
<i>Ribes petraeum</i>	1 –	1 –
<i>Lonicera nigra</i>	1 –	1 –
<i>Sambucus racemosa</i>	1 –	. –
<i>Salix caprea</i>	1 –	. –
<i>Abies alba</i>	1 –	. –
<i>Fagus sylvatica</i>	1 –	. –
<i>Juniperus sibirica</i>	. –	1 –
<i>Betula carpatica</i>	. –	1 –
<i>Larix decidua</i>	. –	1 –
E <sub>1</sub>		
<i>Sorbus aucuparia</i>	<b>87</b> –	<b>89</b> –
<i>Picea abies</i>	<b>61</b> <sup>16.8</sup>	45 –
<i>Pinus cembra</i>	5 –	33 <sup>36.3</sup>
<i>Lonicera nigra</i>	13 –	7 –
<i>Pinus mugo</i>	2 –	14 <sup>23.1</sup>
<i>Ribes petraeum</i>	3 –	4 –
<i>Larix decidua</i>	2 –	3 –
<i>Salix silesiaca</i>	1 –	3 –
<i>Salix sp.</i>	2 –	1 –
<i>Abies alba</i>	5 –	. –
<i>Fagus sylvatica</i>	3 –	. –
<i>Sambucus racemosa</i>	1 –	. –
<i>Juniperus sibirica</i>	. –	3 –
<i>Rosa pendulina</i>	. –	1 –

Group No.	1	2
Differential field layer species (E <sub>1</sub> )		
<i>Athyrium distentifolium</i>	39 <sup>37.1</sup>	8 <sup>-</sup>
<i>Vaccinium vitis-idaea</i>	39 <sup>-</sup>	68 <sup>30.0</sup>
Other field layer species (E <sub>1</sub> )		
<i>Vaccinium myrtillus</i>	<b>98</b> <sup>-</sup>	<b>100</b> <sup>-</sup>
<i>Dryopteris carthusiana</i> agg.	<b>90</b> <sup>-</sup>	<b>89</b> <sup>-</sup>
<i>Homogyne alpina</i>	<b>93</b> <sup>-</sup>	<b>86</b> <sup>-</sup>
<i>Avenella flexuosa</i>	<b>83</b> <sup>-</sup>	<b>97</b> <sup>23.6</sup>
<i>Oxalis acetosella</i>	<b>89</b> <sup>13.7</sup>	<b>79</b> <sup>-</sup>
<i>Calamagrostis villosa</i>	<b>79</b> <sup>-</sup>	<b>70</b> <sup>-</sup>
<i>Luzula sylvatica</i> ssp. <i>sylvatica</i>	<b>76</b> <sup>24.6</sup>	<b>53</b> <sup>-</sup>
<i>Rubus idaeus</i>	48 <sup>-</sup>	<b>59</b> <sup>-</sup>
<i>Luzula luzuloides</i>	42 <sup>-</sup>	<b>51</b> <sup>-</sup>
<i>Adenostyles alliariae</i>	42 <sup>-</sup>	38 <sup>-</sup>
<i>Gentiana asclepiadea</i>	44 <sup>-</sup>	33 <sup>-</sup>
<i>Senecio nemorensis</i> agg.	46 <sup>21.8</sup>	25 <sup>-</sup>
<i>Prenanthes purpurea</i>	33 <sup>-</sup>	22 <sup>-</sup>
<i>Calamagrostis arundinacea</i>	29 <sup>-</sup>	18 <sup>-</sup>
<i>Athyrium filix-femina</i>	28 <sup>18.8</sup>	13 <sup>-</sup>
<i>Solidago virgaurea</i>	19 <sup>-</sup>	24 <sup>-</sup>
<i>Lycopodium annotinum</i>	14 <sup>-</sup>	28 <sup>17.1</sup>
<i>Veratrum album</i> ssp. <i>lobelianum</i>	19 <sup>-</sup>	17 <sup>-</sup>
<i>Huperzia selago</i>	6 <sup>-</sup>	21 <sup>21.3</sup>
<i>Soldanella marmarossiensis</i> agg.	16 <sup>14.4</sup>	7 <sup>-</sup>
<i>Stellaria nemorum</i>	17 <sup>24.6</sup>	3 <sup>-</sup>
<i>Cicerbita alpina</i>	15 <sup>-</sup>	7 <sup>-</sup>
<i>Gymnocarpium dryopteris</i>	13 <sup>-</sup>	7 <sup>-</sup>
<i>Acetosa arifolia</i>	12 <sup>-</sup>	8 <sup>-</sup>
<i>Doronicum austriacum</i>	12 <sup>-</sup>	5 <sup>-</sup>
<i>Milium effusum</i>	11 <sup>-</sup>	4 <sup>-</sup>
<i>Hieracium murorum</i>	6 <sup>-</sup>	11 <sup>-</sup>
<i>Polygonatum verticillatum</i>	7 <sup>-</sup>	4 <sup>-</sup>
<i>Melampyrum sylvaticum</i>	8 <sup>16.3</sup>	1 <sup>-</sup>
<i>Epilobium angustifolium</i>	4 <sup>-</sup>	8 <sup>-</sup>
<i>Gentiana punctata</i>	1 <sup>-</sup>	12 <sup>22.4</sup>
<i>Phegopteris connectilis</i>	4 <sup>-</sup>	5 <sup>-</sup>
<i>Nardus stricta</i>	6 <sup>18.2</sup>	. <sup>-</sup>
<i>Dryopteris filix-mas</i>	5 <sup>-</sup>	3 <sup>-</sup>
<i>Listera cordata</i>	6 <sup>-</sup>	1 <sup>-</sup>
<i>Paris quadrifolia</i>	6 <sup>-</sup>	1 <sup>-</sup>
<i>Carex canescens</i>	6 <sup>16.8</sup>	. <sup>-</sup>
Differential ground layer species (E <sub>0</sub> )		
<i>Lophozia ventricosa</i>	. <sup>-</sup>	24 <sup>36.7</sup>
<i>Bazzania tricrenata</i>	. <sup>-</sup>	22 <sup>35.5</sup>
<i>Mylia taylorii</i>	. <sup>-</sup>	21 <sup>34.3</sup>
<i>Calypogeia integrifolia</i>	12 <sup>-</sup>	39 <sup>31.5</sup>
<i>Cladonia pyxidata</i> ssp. <i>chlorophaea</i>	. <sup>-</sup>	14 <sup>27.9</sup>

Group No.	1	2
<i>Dicranoweisia crispula</i>	.-	13 <sup>26.5</sup>
<i>Barbilophozia attenuata</i>	1-	14 <sup>25.4</sup>
<i>Cladonia digitata</i>	.-	12 <sup>25.1</sup>
<i>Racomitrium microcarpon</i>	.-	12 <sup>25.1</sup>
<i>Diplophyllum taxifolium</i>	.-	12 <sup>25.1</sup>
Other ground layer species ( $E_0$ )		
<i>Dicranum scoparium</i>	<b>81</b> -	<b>93</b> <sup>18.9</sup>
<i>Polytrichum formosum</i>	<b>75</b> -	<b>66</b> -
<i>Plagiothecium curvifolium</i>	41-	<b>50</b> -
<i>Hylocomium splendens</i>	26-	42 <sup>17.3</sup>
<i>Pleurozium schreberi</i>	28-	28-
<i>Sphagnum girgensohnii</i>	17-	30 <sup>16.2</sup>
<i>Rhytidiodelphus triquetrus</i>	15-	16-
<i>Plagiothecium undulatum</i>	15-	11-
<i>Lepidozia reptans</i>	13-	13-
<i>Blepharostoma trichophyllum</i>	11-	14-
<i>Sphagnum capillifolium</i>	15 <sup>15.7</sup>	5-
<i>Tetraphis pellucida</i>	7-	13-
<i>Calypogeia azurea</i>	9-	11-
<i>Polytrichum commune</i>	13-	5-
<i>Plagiomnium affine</i>	12-	7-
<i>Barbilophozia lycopodioides</i>	8-	11-
<i>Dicranella heteromalla</i>	6-	14 <sup>15.0</sup>
<i>Dicranum montanum</i>	9-	7-
<i>Cetraria islandica</i>	3-	14 <sup>20.9</sup>
<i>Lophozia cf. incisa</i>	8 <sup>16.3</sup>	1-
<i>Rhytidiodelphus squarrosus</i>	8 <sup>16.3</sup>	1-
<i>Plagiochila porelloides</i>	8 <sup>16.3</sup>	1-
<i>Hypnum cupressiforme</i>	2-	11 <sup>18.0</sup>
<i>Plagiothecium denticulatum</i>	7-	1-
<i>Ditrichum heteromallum</i>	.-	11 <sup>23.6</sup>
<i>Cladonia gracilis</i>	1-	8 <sup>17.0</sup>
<i>Anastrepta orcadensis</i>	.-	9 <sup>22.0</sup>
<i>Lophozia sudetica</i>	.-	9 <sup>22.0</sup>
<i>Cladonia coccifera</i>	.-	9 <sup>22.0</sup>
<i>Plagiothecium laetum</i>	6 <sup>16.8</sup>	.-
<i>Brachythecium starkei</i>	5-	1-
<i>Cladonia squamosa</i>	1-	7 <sup>14.9</sup>
<i>Ptilidium ciliare</i>	1-	7 <sup>14.9</sup>
<i>Bazzania trilobata</i>	3-	4-
<i>Polytrichum juniperinum</i>	1-	7 <sup>14.9</sup>
<i>Cladonia rangiferina</i>	.-	7 <sup>18.4</sup>

(D) Another example of geographically separated vicariant unit (of the alliance *Piceion abietis*) is the group of Scandinavian Norway spruce communities, recognized as the alliance *Linnaeo borealis-Piceion abietis* Oberdorfer ex Jahn 1985<sup>26</sup> (JAHN 1985; KIELLAND-LUND 1981, 1994; DIERSSEN & DIERSSEN 1996). While still integral part of the order *Piceetalia abietis*, its differential species including *Trientalis europaea* (as constant species) and especially *Linnaea borealis* represent phytochorological relation to East European-Siberian taiga woodlands of the class *Piceo obovatae-Abietetea sibiricae* (see above).

The natural altitudinal distribution of Scandinavian Norway spruce woodland is considerably influenced by pre-/historical deforestation and pasture. Within the upper part of its potential natural distribution, large-scale substitutionary non-forest vegetation is developed, in abandoned places evolution of secondary and temporary birch phytocoenoses is in progress. Currently, Norway spruce is only artificially planted in the relevant altitudes, mostly in very small stands (Kučera, not.). On the contrary, large-scale Norway spruce forests of lower altitudes, especially in the southern part of Scandinavia, are replacing mixed broadleaved woodland of *Quercus*, *Fagus*, *Acer* spp. etc. of much larger potential natural distribution.

(E) MUCINA et al. (2016) include in the order *Piceetalia abietis* also the alliance *Pinion peucis Horvat 1950* from the Southern Balkans comprising acid Macedonian-pine woodlands.

(F) Similar as in detail explained in the survey on calcareous Norway spruce woodlands of Slovakia (KUČERA 2022; see also above), incorrect syntaxonomical classification of the Norway spruce forest stands with direct anthropogenic as well as subanthropogenic origin is frequently found in the literature dealing with acid Norway spruce vegetation types. Numerous non-calcareous *Picea abies* forest stands of the Western Carpathians are secondary forest communities with the spontaneous secondary succession of *Fagus sylvatica*, and they should be syntaxonomically classified within the class *Carpino-Fagetea*.

Therefore, the total number of available records of authentic *Piceetalia abietis* woodlands is much smaller than commonly expected not only within the Western Carpathians (see Table 1 and the accompanying text) but undoubtedly also in other European regions. One of the latest examples of inappropriate evaluation is a statement that *Piceion abietis* phytocoenoses (with the occurrence of *Soldanella carpatica*) are in the Western Carpathians distributed already at the altitude of 940 m a.s.l.<sup>27</sup> (VALACHOVIČ et al. 2019). All parallel records of non-natural and assumed natural acid Norway spruce forests – but in fact anthropogenically changed *Carpino-Fagetea* phytocoenoses – from other European mountain ranges should be syntaxonomically re-evaluated.

(G) True bog woodlands with *Pinus sylvestris*, Central European *P. hartenbergiensis* Liebich (*P. rotundata* auct. non Link, cf. BUSINSKÝ & KIRSCHNER 2006) and various *Pinus* hybrids

<sup>26</sup> See JAHN (1985: 36); syn.: *Linnaeo borealis-Piceion* Oberdorfer 1979 nom. inval. (Art. 2b), OBERDORFER (1979: 45) rather as an alternative name (cf. THEURILLAT et al. 2021: 17) than a nomen novum; corresp. name: *Linnaeo-Piceenion* (Br.-Bl. et Sissingh in Br.-Bl. et al. 1939) Förster in Jahn 1977 (JAHN 1977: 486); non: *Linnaeo-Piceon abietis* (Br.-Bl. et Sissingh in Br.-Bl. et al. 1939) Rivas-Mart. in Rivas-Mart. et al. 2011 nom. illeg. (cf. KUČERA 2022).

<sup>27</sup> The respective record and all similar ones of low montane altitudes represent anthropogenically changed *Carpino-Fagetea* phytocoenoses. Moreover, the relevé under consideration (i.e. VALACHOVIČ & JAROLÍMEK 1988: 14) does not belong to the vegetation type of acid woodland phytocoenoses, where *Piceion abietis* is assigned: the correct syntaxonomical evaluation is within calcareous woodlands of the order *Cephalanthero damasonii-Fagetalia sylvaticae* Boeuf et Royer in Boeuf et al. 2014. At the same time, this relevé should also be included in Tab. 1/Part 1 published by KUČERA (2022).

(cf. BUSINSKÝ & KIRSCHNER 2010), marginally also with *Betula pubescens* (in some regions *Betula carpatica* is also referred: e.g. ŠMARDA 1950; DIERSSEN & DIERSSEN 1984) and/or *Picea abies*, usually classified within the class *Vaccinio-Piceetea* (WALLNÖFER 1993; THEURILLAT et al. 1995; JIRÁSEK & MORAVEC 2002; JAROLÍMEK et al. 2008b; CHYTRÝ et al. 2013b;<sup>28</sup> CHIFU 2014; COLDEA 2015; MUCINA et al. 2016), represent a group of an ecologically, geobotanically and floristically distinct woodland types unit classified as separate class *Vaccinio uliginosi-Pinetea* Passarge 1968 (PASSARGE 1968; PASSARGE & HOFMANN 1968; KUČERA 2007; WILLNER & STEINER 2007; RENAUD 2015).

In the Western Carpathians, partly marginal syntaxonomical position within the latter class – and within the order *Vaccinio uliginosi-Pinetaea* Passarge 1968 (cf. WILLNER & STEINER 2007) – take *Betula pubescens* phytocoenoses recorded by ŠOMŠÁK (1979) and included by him to the association '*Eriophoro vaginati-Betuletum* Hueck 1925 em. Passarge et Hofmann 1968'. Similar as in the case of the association *Sphagno palustris-Piceetum* Šomšák 1979 (order *Sphagno palustris-Piceetalia* P. Kučera 2019), some relevés have a transitional position towards the class *Alnetea glutinosae* Br.-Bl. et Tx. ex Westhoff et al. 1946. However, a large number of the later recorded relevés referred to Šomšák's unit by Slovak authors, including by Šomšák himself, are not bog phytocoenoses and they belong to the order *Sphagno palustris-Piceetalia* (see the syntaxonomical revision by KUČERA 2019b). Other part of *Betula pubescens* mire (non-true bog) phytocoenoses from Slovakia form a nutrient-poorer section of the class *Alnetea glutinosae* Br.-Bl. et Tx. ex Westhoff et al. 1946 (incl. *Molinio-Betuletalia pubescentis* Passarge 1968) (cf. FRANZ & WILLNER 2007; RENAUD 2015).

(H) Floristically and ecologically specific communities of waterlogged (mixed) Norway spruce woodlands are traditionally classified within the order *Piceetalia abietis* as well, for example *Bazanio-Piceetum* auct. non (Schmid et Gaisberg 1936) Br.-Bl. et Sissingh in Br.-Bl. et al. 1939, *Equiseto sylvatici-Piceetum* Šmarda 1950, *Soldanello montanae-Piceetum* Volk in Br.-Bl. et al. 1939 and *Sphagno palustris-Piceetum* Šomšák 1979 (OBERDORFER 1957; OBERDORFER et al. 1967; ŠOMŠÁK in MUCINA et al. 1985; POTT 1992; SEIBERT 1992; WALLNÖFER 1993; JIRÁSEK 1996, 2002; SHELYAG-SOSONKO et al. 2006; EXNER 2007; JAROLÍMEK et al. 2008a; SOLOMAKHA 2008; KUČERA 2012a; CHYTRÝ et al. 2013; cf. also DUBYNA et al. 2019). Based on their substantial phytocoenological differences from the group of supramontane hillside acid Norway spruce woodlands, KUČERA (2019b) separated them to an independent order *Sphagno palustris-Piceetalia* P. Kučera 2019, which should be syntaxonomically included as an independent order into the class *Vaccinio uliginosi-Pinetea* Passarge 1968 (cf. KUČERA 2007).<sup>29</sup> However, the association *Sphagno capillifolii-Piceetum* Zukrigl 1973 syntaxonomically belongs to the order *Piceetalia abietis*, even if the community represents marginal phytocoenoses of the alliance *Piceion abietis* (KUČERA 2019b).

*Syntaxonomical note.* – The alliance *Athyrio alpestris-Piceion* Sýkora 1971 based on floristically poor phytocoenoses recorded by SÝKORA (1971) is not distinguished as an independent unit of the order *Piceetalia abietis* in this syntaxonomical survey due to absence of the sufficient floristical

<sup>28</sup> In this survey is, however, only one part of woodland (and scrub) bog communities of the Czech Republic included: the other part was elaborated within non-forest communities of the class *Oxycocco-Sphagnetea* Br.-Bl. et Tx. ex Westhoff et al. 1946 (HÁJKOVÁ et al. 2011).

<sup>29</sup> In this way, equivalently to the class *Vaccinio-Piceetea* consisting of two orders considerably differing in their nutrient (and calcium) supply, the classes *Vaccinio uliginosi-Pinetea* and *Alnetea glutinosae* would have broader syntaxonomical content and geobotanical application as well.

differentiation in comparison to the alliance *Piceion abietis* (ŠOMŠÁK 1983; EXNER 2007; KUČERA 2010a, 2010b, 2012a; CHYTRÝ et al. 2013b). However, closer examination should be devoted to field research and possible differentiation of group of species-richer syntaxa as, for example, the associations *Solidagini-Piceetum* and *Parido-Piceetum* and their equivalents in other European regions.

MUCINA et al. (2016) incorrectly associated the name *Athyrio alpestris-Piceion* Sýkora 1971 as a synonym of the alliance name *Chrysanthemo rotundifolii-Piceion* (Krajina 1933) Březina et Hadač in Hadač 1962 nom. superfl. = *Chrysanthemion rotundifolii* Krajina 1933 (cf. KUČERA 2023).

### 3.2. *Piceion abietis* Pawłowski ex Pawłowski et al. 1928 nom. corr.

Nomenclatural type: association *Piceetum excelsae* Pawłowski ex Pawłowski et al. 1928<sup>30</sup> (PAWŁOWSKI et al. 1928: 257), automatic holotype (Art. 18).

Original name: *Piceion excelsae* Pawłowski ex Pawłowski et al. 1928 nom. inept. (Art. 44) (Pawłowski et al. 1928: 218–219, 257)

Nomencl. syn.: *Vaccinion myrtilli* Krajina 1933 p. p. = typus excl. (see KRAJINA 1933: 152, 195 vs. ŠIBÍK et al. 2007) = *Myrtillo-Piceion excelsae* Březina et Hadač in Hadač 1962 nom. superfl.<sup>31</sup> (Art. 10, 14b, 29c)

Syntax. syn.: *Piceion excelsae* Sillinger 1933 p. p. min., *Vaccinio-Piceion excelsae* Br.-Bl. in Br.-Bl. et al. 1939 p. p. min.,<sup>32</sup> *Athyrio alpestris-Piceion* Sýkora 1971

Non: *Piceion excelsae* Luquet 1926 nom. inval. (Art. 3f),<sup>33</sup> *Piceion excelsae* Br.-Bl. 1930 nom. inval. (Art. 2b, 8),

*Chrysanthemion rotundifolii* Krajina 1933 = *Chrysanthemo-Piceion* (Krajina 1933) Březina et Hadač 1962 nom. superfl. (Art. 29c) = *Adenostylo-Piceenion* Borhidi 1969, *Oxalidion acetosellae* Krajina 1933 nom. illeg. (Art. 29b) = *Oxalido-Piceion* (Krajina 1933) Březina et Hadač in Hadač 1962,

*Chrysanthemo-Piceion* auct. non (Krajina 1933) Březina et Hadač in Hadač 1962, *Oxalido-Piceion* sensu Hadač et al. 1969 non Březina et Hadač in Hadač 1962,

*Vaccinio vitis-idaeae-Piceion* (Br.-Bl. in Br.-Bl. et al. 1939) Passarge 1971 p. p. max.,<sup>34</sup> *Luzulo*

<sup>30</sup> The nomenclatural type of this association was selected by WALLNÖFER (1993: 287).

<sup>31</sup> See above comment on the name *Myrtillo-Piceetalia excelsae* Hadač 1962.

<sup>32</sup> See the very wide original syntaxonomical content of BRAUN-BLANQUET et al. (1939), including not only coniferous substitutionary *Carpino-Fagetea* woodlands and *Cortuso matthioli-Piceetalia abietis* communities, but also some scrub and non-forest communities.

<sup>33</sup> Although the chapter on *Piceion excelsae* contains a reference to the unit '*Piceo-Abietetum albae* Szafer et al. 1923' (LUQUET 1926: 164; THÉBAUD & BERNARD 2018), this citation is a reference to a compared vegetation type and not an element of the original diagnosis of the alliance name (cf. also KUČERA 2012a: 177). Moreover, considering the methodical approach of SZAFAER et al. (1923), their new association names are not validly published (Art. 2b → Art. 7) as a 'relevé' in the sense of SZAFAER et al. (1923: 13) consists, in fact, from set of 5 to 25 small plots (KUČERA 2007).

<sup>34</sup> Change of the name *Vaccinio-Piceion* Br.-Bl. in Br.-Bl. et al. 1939 to the form '*Vaccinio vitis-idaeae-Piceion*' by PASSARGE (1971) should not be considered as an alliance name completion according to Rec. 10C, because the survey of BRAUN-BLANQUET et al. (1939) does not provide a key to such completion (cf. Art. 3g). Considering the new syntaxonomical classification by PASSARGE (1971) (cf. also Art. 47), the new Passarge's alliance has considerably narrowed syntaxonomical content and does not include the nomenclatural type of the name *Vaccinio-Piceion* Br.-Bl. in Br.-Bl. et al. 1939 (cf. DENGLER et al. 2004). However, the original alliance name '*Vaccinio-Piceion* Br.-Bl. in Br.-Bl. et al. 1939' was not retained according to the Art. 24 by PASSARGE (1971) for any other alliance.

*luzuloidis-Piceion abietis* Passarge 1971 nom. corr. (Rec. 10C, Art. 44) p. p. max.,<sup>35</sup> *Oxalido-Piceion* (Krajina 1933) Passarge 1971 nom. illeg. (Art. 31) p. p. max.

Differential species (see Table 3): *Athyrium distentifolium* (mostly negative to quantitative species differentiation).

*Floristical delimitation.* – The canopy dominant species is *Picea abies*, *Sorbus aucuparia* (usually ssp. *glabrata*) is constantly admixed. Within the Western Carpathians (and for example in the Alps), *Larix decidua* is a natural component of stands in the region of Tatra Mts, in some habitats permanently also *Betula carpatica*. *Larix* and *Sorbus* (and on the respective localities also *Betula*) have increased abundance in successional stages of stands influenced by wind and other natural disturbances. *L. decidua* had probably the same distribution pattern also within *Piceion abietis* communities of the Low Tatra Mts. The stands of the lower part of the altitudinal distribution of the *Piceion abietis* woodlands were enriched by natural presence of *Abies alba*,<sup>36</sup> in some localities *Acer pseudoplatanus* was probably present, marginally also *Fagus sylvatica* of lower growth and without an ecological influence on the development and species diversity of phytocoenoses.

Careful consideration of progressive spontaneous secondary succession of *F. sylvatica* in *Picea* stands is needed, because this process indicates considerable anthropogenically influenced forests in habitats, where the potential natural vegetation is a mixed *Fagus-Abies(-Picea)* woodland of the class *Carpino Fagetea*. Such phytocoenoses represent temporary *Picea abies* communities which should be correctly classified within the latter class. It would be incorrect to label the described vegetation change as cessation of Norway spruce stands of lower altitudes due to climate change. For such evaluation detailed field study of localities of natural altitudinal transition of natural upper montane mixed acid *Fagus* woodland into natural supramontane acid *Picea* woodland are required. However, such stands were not preserved within the Western Carpathians and, moreover, the altitude ca. 1250 m a.s.l. generally assumed to be the natural lower limit of altitudinal distribution of Norway spruce woodlands does not correspond to recent field revisions (see above and KUČERA 2012a, 2013a, 2014, 2015, 2022).

In addition, woodlands with a permanent natural occurrence of *Pinus cembra* in the canopy belong to the alliance *Homogyno alpinae-Pinion cembrae* P. Kučera 2017 (cf. KUČERA 2022). *P. cembra* could be present in *Piceion abietis* communities only as temporary species occurrence – mostly of anthropogenic origin. Such plantations are locally found within the High Tatras in the region of the Štrbské pleso Lake or in the Mengusovská dolina Valley (2.10.2020, Kučera, not.)

In the understorey of *Piceion abietis* coomunities are, especially in the region of the Tatra Mountains, occasionally admixed other woody species (*Lonicera nigra*, *Sambucus racemosa*, *Ribes petraeum*), including *Pinus mugo* permanently present in the ecologically more extreme habitats.

<sup>35</sup> THÉBAUD & BERNARD (2018) used and lectotypified the name '*Luzulo luzuloidis-Piceion abietis* Passarge 1978'. However, PASSARGE (1971) validly published the relevant name already earlier (i.e. *Luzulo nemorosae-Piceion abietis* Passarge 1971 nom. inept. [Rec. 10C, Art. 44]) and it is automatically typified with the name *Luzulo nemorosae* (Schmid et Gaisberg 1936) Br.-Bl. et Sissingh in Br.-Bl. et al. 1939. According to the phytocoenotic content of the latter association name as well its nomenclatural type (see KUČERA 2010a: 834), the considered association belongs to the class *Carpino-Fagetea*, because the original relevé records represent an anthropogenically changed substitutionary woodland (cf. KUČERA 2022).

<sup>36</sup> Sporadic trees were found in the Western Carpathians in acid habitats even above 1500 m a.s.l. (cf. KUČERA 2012a, 2021), similarly in the easternmost part of the Alps (ZUKRIGL 1973).

The field layer species composition of the alliance *Piceion abietis* is – especially within the Western Carpathians and Hercynian mountain ranges with impoverished flora in comparison to the Alps and Southern Carpathians – characterized by the absence of distinct Braun-Blanquetian character-species sensu stricto. The differentiation against the alliance *Homogyno alpinae-Pinion cembrae* is represented only by mostly a small difference in frequency of species and absence of high-mountain species (KUČERA 2017; ZIĘBA et al. 2018).

The basis of species composition of the most widespread communities consists of *Vaccinium myrtillus*, *Calamagrostis villosa*, *Homogyne alpina*, *Oxalis acetosella*, *Luzula sylvatica* ssp. *sylvatica* and taxa of *Dryopteris carthusiana* agg. (especially *Dryopteris expansa* and hybrids are not sufficiently recognized to the present). Species like *Athyrium distentifolium*, *V. vitis-idaea*, *Gentiana asclepiadea*, *Rubus idaeus*, *Prenanthes purpurea* are less abundant. Other species are more or less bound to specific habitat types (e.g. *Acetosa arifolia*, *Adenostyles alliariae*, *Luzula luzuloides*, *Solidago virgaurea*, *Veratrum album* ssp. *lobelianum*), eventually they are also restricted to a special distribution pattern (*Athyrium filix-femina*, *Calamagrostis arundinacea*, *Melampyrum sylvaticum*, *Paris quadrifolia*) (KUČERA et al. 2023). Phytocoenoses with admixed *Carex canescens*, *C. echinata*, *Eriophorum vaginatum* have a marginal syntaxonomical position within the alliance *Piceion abietis* (KUČERA 2019b).

In contrast to the mountain ranges lying more to the west, the hitherto known Western Carpathian records of the natural acid *Piceion abietis* communities only sporadically document the occurrence of *Trientalis europea* and only very rarely species *Blechnum spicant*, *Streptopus amplexifolius*, *Polygonatum verticillatum*. The same is valid for moss species including *Barbilophozia lycopodioides*, *Bazzania trilobata*, *Rhytidadelphus loreus* (cf. MATUSZKIEWICZ & MATUSZKIEWICZ 1960; HARTMANN & JAHN 1967; SEIBERT 1992; WILLNER et al. 2007; CHYTRÝ et al. 2013b).

Similarly to the field layer, the ground layer of *Piceion abietis* phytocoenoses is not characterized by distinct differential species. Commonly distributed mosses *Dicranum scoparium* and *Polytrichum formosum* represent the usual constant species, higher frequency values are reached by *Plagiothecium curvifolium* and *Pleurozium schreberi*. Several woodland types are characterized by abundant *Sphagnum girgensohnii* and *S. capillifolium*. Occurrence of species as *Hylocomium splendens*, *Rhytidadelphus triquetrus*, *Polytrichum commune*, *Anastrophyllum minutum*, *Plagiochila porelloides* is bound to ecological specific habitat types (e.g. scree, waterlogged soils). Other bryophyte species are present only with low frequency or sporadically, including *Lepidozia reptans*, *Calypogeia integriflora*, *Plagiomnium affine*, *Plagiothecium undulatum*, *Rhytidadelphus squarrosum* etc. Lichens occur in *Piceion abietis* communities only rarely as elements of the ground layer flora (*Cetraria islandica*, *Cladonia* spp.).

*Distribution, ecological delimitation.* – The alliance *Piceion abietis* comprises mountain woodlands of natural Norway spruce phytocoenoses bound to considerably nutrient-poor habitats. As such they represent ecological vicariant to the *Cortuso matthioli-Piceion* woodlands.

The communities of *Piceion abietis* are widely distributed within different parts of European mountain systems. On the respective geological background they form a more or less continuous zone in the Alps from France to Slovenia (WALLNÖFER 1993; KELLER et al. 1998; PIGNATTI 1998, ZUPANČIČ 1999; EXNER 2007; THÉBAUD & BERNARD 2018) including the Pohorje Mts (WRABER 1960, 1963). Within the Hercynian orographical system, the natural Norway spruce woodlands are fragmented into usually distant isolated islands due to the considerable lower total

altitude of the individual mountain ranges, including the Harz Mts, where the occurrence of natural Norway spruce woodland is also referred (SEIBERT 1992; MATUSZKIEWICZ 2002; SAUTTER 2003; EXNER 2007; EWALD et al. 2011; CHYTRÝ et al. 2013b). The communities of this alliance are also distributed in all main units of the Carpathians: in the Western Carpathians (ŠOLTÉS 1976; MATUSZKIEWICZ 2002; KUČERA 2012a) as well as in the Eastern and Southern Carpathians (BORHIDI 1971; SHELYAG-SOSONKO et al. 2006; CHIFU 2014; COLDEA 2015; DUBYNA et al. 2019).

On the example of the Hercynian system could be explained the importance of distinction between (A) regions with occurrence of true supramontane acid Norway spruce woodland (alliance *Piceion abietis*) including the Harz Mts, the High Sudetes, the Bohemian Forest (BRAUN-BLANQUET et al. 1939; KLIKA 1944; OBERDORFER 1957; MATUSZKIEWICZ & MATUSZKIEWICZ 1960; HARTMANN & JAHN 1967; MATUSZKIEWICZ 1977, 2002; SOFRON 1981; POTT 1992; SEIBERT 1992; WALLNÖFER 1993; JIRÁSEK 1996, 2002; EXNER 2007; CHYTRÝ et al. 2013b) and (B) regions where the natural occurrence of *Picea abies* is preserved (occasionally only in specific habitats such as mires), however, the altitudinal vegetation zone of supramontane Norway spruce woodland is not naturally developed, for example the Vosges, the Black Forest, the Thuringian Forest (cf. BARTSCH & BARTSCH 1940; ISSLER 1942; SCHLÜTER 1966; KUČERA 2012a).

Their differentiation is complicated by thousands of years of anthropogenic impacts, i.e. including considerable prehistorical deforestation (cf. SHENNAN 1993, ELLENBERG 1996, KAPLAN et al. 2009, 2016; KOLÁŘ et al. 2018) which, eventually, influenced species composition of Central European mountain woodlands (especially in favour of *P. abies*) as well as by establishment of Norway spruce monocultures long before the 20<sup>th</sup> century (for comparison in the region of the Western Carpathians see: LOŽEK 1973, 2007; OBUCH et al. 2008; OBUCH 2021; PIETA 2010). These two long-term impacts caused the change of undergrowth phytocoenoses resulting in the imitation of *Piceion abietis* communities (cf. HADAČ & SOFRON 1980 vs. KUČERA 2012a).

The lower line of altitudinal distribution of the *Piceion abietis* communities in the Carpathian and Hercynian mountain ranges is limited by occurrence of the natural upper montane mixed *Fagus sylvatica* woodland of the class *Carpino-Fagetea* (including substitutionary secondary successional *Picea abies* stands of subanthropogenic and direct anthropogenic origin [plantations] with various stages of the progressive recovery of a respective mixed *Fagus* woodland type).

Within the Western Carpathians, the natural acid Norway spruce communities are usually widespread above ca. 1400 m a.s.l. forming a separate altitudinal vegetation zone, similarly as in the case of *Cortuso matthioli-Piceion* (KUČERA 2012a, 2013a, 2014). They are descending into lower altitudes only under influence of extreme habitat conditions, generally on screes with various boulder sizes, in glacially formed valleys of the Tatra Mountains even in spatially more continuous stands. Spatially extensive Norway spruce stands of lower altitudes outside of such specific habitats as well as in lower mountain ranges (e.g. the Kysucké Beskydy Mts, the Branisko Mts., the Klenovský Vepor Mts etc.) have usually significant secondary successional character (progressive reverse spontaneous succession of *Fagus*), therefore they do not belong to the class *Vaccinio-Piceetea*: they represent above-mentioned substitutionary *Picea* forests (KUČERA 2012a, 2022). Within the Poľana Mts, natural Norway spruce communities were probably spatially limited to more extreme habitats only as the natural distribution of mixed (*Fagus-Abies-Picea*) woodland ascended up the peak of Poľana Mt. (KUČERA 2011b, 2012a).

The elevational span of the Norway spruce altitudinal vegetation zone has three main types within individual mountain ranges of the Western Carpathians (KUČERA 2022):

- (1) the respective supramontane Norway spruce zone is limited by the total height of the individual summits: the mittelgebirge mountain ranges which do not exceed the alpine forest line – for example the Veporské vrchy Mts (Fabova hoľa-group), the Stolické vrchy Mts (Stolica–Kohút group);
- (2) the supramontane Norway spruce zone is fully developed and the alpine forest line is formed by *Picea abies* (originally above 1700 m a.s.l., locally lower under the influence of summit syndrome or unsuitable soil conditions; cf. KÖRNER 2012): the mittelgebirge mountain ranges with the highest isolated summits or more continuous areas exceeding this line – for example the Oravské Beskydy Mts or the Low Tatras (Nízke Tatry Mts; with transitional character to a hochgebirge mountain range);
- (3) the alpine forest line is formed by (mixed) *Pinus cembra* communities: the hochgebirge mountain ranges which provided a postglacial refugium for survival of *Pinus cembra* populations – the individual regions of the Tatra Mountains. Here the elevation span of natural Norway spruce communities was originally limited by abundant development of the *Homogyno alpinae-Pinion cembrae* P. Kučera 2017 (and calcicolous *Calamagrostio variae-Pinion cembrae* P. Kučera 2017) communities which, however, were preserved only in fragments until the middle of the 20<sup>th</sup> century (ZIEBA et al. 2018; KUČERA 2019a). Therefore, the *Picea(-Larix)* stands of the Tatra Mountains ascend secondarily higher, partially with support of artificial reforestation, also above the altitudes 1550–1650 m a.s.l., replacing the former natural mixed *Pinus cembra* communities (KUČERA 2012a; cf. BRAUN-BLANQUET 1930; SOMORA 1969, 1976, 1977; PLESNÍK 1971; SOMORA & HUMLOVÁ 1971).

The natural alpine forest line is preserved only exceptionally within the Western Carpathians (the frame of climate conditions is considered for the period 1950–1980). Current Norway spruce stands vertically (locally also horizontally) border sub-/anthropogenic *Pinus mugo* stands or remnants and various successional stages of the former high-mountain pastures, usually with a transitional spontaneous woodland recovery zone (cf. KUČERA 2019a vs. relevés of KRAJINA 1933).

*Syntaxonomical delimitation.* – The currently accepted syntaxonomical content of the alliance *Piceion abietis* is considerably narrowed in comparison to historical conceptions (PAWŁOWSKI et al. 1928; BRAUN-BLANQUET et al. 1939; KLIKA 1944 vs. HADAČ 1962 to MUCINA et al. 2016), because the calcareous *Picea* phytocoenoses are excluded in the order *Cortuso matthioli-Piceetalia* (= *Athyrio-Piceetalia* auct. non Hadač 1962). Also wet Norway spruce woodlands on mire habitats were recognized as a separate unit on the rank of order (KUČERA 2019b). Similarly, acid Arolla pine communities have to be separated as well (KUČERA 2017).

The most serious and most frequent question is a proper as well as essential distinction between natural acid Norway spruce communities (class *Vaccinio-Piceetea*) and various types of substitutionary Norway spruce stands replacing former natural (mixed) *Fagus(-Abies-Picea)* woodlands (class *Carpino-Fagetea*) (see above and KUČERA 2012a, 2022). In addition to Table 1, the following chapter illustrates examples of disputable syntaxa from various European regions (cf. also KUČERA 2012a, chapter).

*Syntaxonomical note.* – PASSARGE (1971) proposed splitting of all European Norway spruce communities historically included to one alliance *Piceion abietis* (ut *Vaccinio-Piceion* Br.-Bl. in Br.-Bl. et al. 1939) into three trophically different alliances labelled *Vaccinio vitis-idaeae-Piceion*, *Luzulo nemorosae-Piceion* and *Oxalido-Piceion*;<sup>37</sup> however, calcareous Norway spruce communities were not properly recognized as a separate unit. Even if his original intention of classification reflects on general logical division according to nutrient-supply of habitats, the floristical differentiation of true natural acid Norway spruce communities of Central Europe in the present included within the alliance *Piceion abietis* seems not convincing in favour of differentiation of such three alliances. Moreover, the considerable number of subordinated syntaxa considered by PASSARGE (1971) belong syntaxonomically and phytocorologically either to other alliances than *Piceion abietis* (see above) or, in fact, outside the class *Vaccinio-Piceetea* – most frequently to *Carpino-Fagetea* (cf. also KUČERA 2012a, 2019b).

*Nomenclatural note 1.* – WILLNER (2007: 239) evaluated the name *Piceion excelsae* Pawłowski ex Pawłowski et al. 1928 (nom. inept.) formed from the name of one species only (*Picea excelsa* Link, nom. illeg.) as misleading. Therefore, he proposed the conservation of younger name *Vaccinio-Piceion* Br.-Bl. in Br.-Bl. et al. 1939. Considering all current knowledge, this proposal has to be considered as unnecessary and superfluous because the nomenclatural and syntaxonomical application of the name *Piceion excelsae* Pawłowski ex Pawłowski et al. 1928 is unambiguously and clearly determined by its nomenclatural type belonging to natural acid Norway spruce community: “Names are only labels (...) It is far more important to know exactly what is meant by a name than to find one that seems in every respect to be characteristic.” (WEBER et al. 2000: 740; KUČERA 2012a: 177).

*Nomenclatural note 2.* – WILLNER (2007: 239) considered the alliance *Oxalido-Piceion* (Krajina 1933) Březina et Hadač in Hadač 1962 (= *Oxalidion acetosellae* Krajina 1933 nom. illeg., Art. 29b) to be homotypic with *Piceion excelsae* Pawłowski ex Pawłowski et al. 1928 nom. inept. However, as the alliance *Piceion abietis* is formally mediated by the subassociation *Piceetum myrtilletosum* Pawłowski et al. 1928 (WALLNÖFER 1993: 287) and KRAJINA (1933: 152) proposed his alliance *Oxalidion acetosellae* on a base of division of the *Piceion abietis* alliance and unambiguous exclusion of the considered *Piceetum myrtilletosum* Pawłowski et al. 1928 from *Oxalidion acetosellae*, thus Willner’s respective nomenclatural evaluation is incorrect.

#### 4. Selected examples of commonly assumed natural Norway spruce communities

(I) The classical case of secondary non-natural Norway spruce forests derived from *Carpino-Fagetea* communities represent records of *Piceetum excelsae* (especially *Piceetum normale* sensu Szafer et al. non Beger 1922) and *Piceo-Abietetum albae* published by SZAFAŘEK et al. (1923) from the montane altitudes of the Dolina Chochołowska Valley (the Western Tatras, Poland). The whole region was strongly influenced by historical deforestation, high-mountain pasture and forest exploitation due to mining-related activities. As a result, *Fagus* population was completely destroyed at the time within the whole valley (SZAFAŘEK et al. 1923; HOŁUB-PACEWICZOWA 1931; FABIJANOWSKI 1962) and the *Fagus* phytocoenoses, more or less degraded by historical land management, were in the beginning of the 20<sup>th</sup> century preserved only in the adjacent territories in Poland and Slovakia (SZAFAŘEK et al. 1927a; SVOBODA 1939; ČERNUŠÁKOVÁ & DOBŠOVÍČOVÁ 2005; KUČERA

<sup>37</sup> The important syntaxonomical proposals published by HADAČ (1962) and HADAČ et al. (1969) were not taken into account; partially only in the author’s later paper (PASSARGE 1978).

2012a; OCIEPA et al. 2020; PIELECH et al. 2021). The anthropogenic origin of the considered *Picea* and *Picea-Abies* forests of the Dolina Chochołowska Valley was correctly identified already by SZAFAŘ ET AL. (1927b).

(II) *Hieracio transsilvanici-Piceetum* Pawłowski et Br.-Bl. in Br.-Bl. et al. 1939 nom. corr. (*Hieracio rotundatae-Piceetum* Pawłowski et Br.-Bl. in Br.-Bl. et al. 1939 nom. inept., resp. *Hieracio rotundatae-Piceetum* (Zlatník 1935) Pawłowski et Br.-Bl. in Br.-Bl. et al. 1939 nom. inept.)<sup>38</sup> described from the Eastern Carpathians is at least partially based on upper montane degraded mixed *Fagus* forests and substitutionary *Picea* forests. This evaluation could be supported by presence of species as *Anemone nemorosa*, *Galeopsis speciosa* or high constancy of *Calamagrostis arundinacea* or *Athyrium filix-femina* (see ZLATNÍK 1935), both unusual for parallel Western Carpathian mittelgebirge mountain ranges. Detailed reconsideration of the real natural distribution of supramontane (i.e. natural) Norway spruce woodlands – equivalent to the one made for the Western Carpathians (KUČERA 2012a) – should be realized.

(III) *Luzulo luzuloidis-Piceetum* (Schmid et Gaisberg 1936) Br.-Bl. et Sissingh in Br.-Bl. et al. 1939 nom. corr. (see comments below under 'A') and *Bazzanio trilobatae-Piceetum* (Schmid et Gaisberg 1936) Br.-Bl. et Sissingh in Br.-Bl. et al. 1939 nom. corr. (*Mastigobryo-Piceetum* (Schmid et Gaisberg 1936) Br.-Bl. et Sissingh in Br.-Bl. et al. 1939 nom. inept.) (see comments below under 'B') are two communities originally described from the Northern Black Forest (southwest Germany). Up to the present, both names (or at least the second one) are applied for true *Vaccinio-Piceetea* woodlands (cf. POTT 1992; SEIBERT 1992; WALLNÖFER 1993; EXNER 2007; BERGMEIER 2020).

However, little attention was paid to the fact that the original relevé data of both associations as well as other communities published by SCHMID & GAISBERG (1936, relevé tables II–VI) were recorded purposefully on carefully selected relevé plots limited to the phytocoenoses dominated by *Picea abies* regardless of their naturalness (see SCHMID & GAISBERG 1936: 28). For this reason, the relevés of OBERDORFER (1938, tabs. 24, 25) and BARTSCH & BARTSCH (1940, tabs. 20, 21) represent vegetation records partially less biased in respect of tree species occurrences which also influenced the overall recorded species richness. More numerous and phytocoenotically diverse records of the woodland cover of the Northern Black Forest were published by MURMANN-KRISTEN (1987), including various *Fagus* and *Abies* phytocoenoses.

As seen from most of the later various geobotanical applications (cf. SEIBERT 1992; KUČERA 2007, 2012a: 241–242 and 2019b, Suppl. 3/sect. II), the artificial phytocoenotical character of the original diagnoses of *Luzulo luzuloidis-Piceetum* and *Bazzanio-Piceetum* was neglected and, for example, in the lands of former Czechoslovakia the latter association was commonly understood as a natural wetland *Picea* community, i.e. for the most part as pseudonym *Bazzanio trilobatae-Piceetum* auct. non (Schmid et Gaisberg 1936) Br.-Bl. et Sissingh in Br.-Bl. et al. 1939 s. str. This association was understood by some German authors in the same way (e.g. SCHLÜTER 1969; DIERSSEN & DIERSSEN 1984; MURMANN-KRISTEN 1987); on the contrary, such wetland

<sup>38</sup> The formal validity of names published by ZLATNÍK (1935) (for example, *Dentario bulbiferae-Fagetum* Zlatník 1935) could still be disputable: even though the synoptic tables 1 and 2 of ZLATNÍK (1935, beginning after page 122) only contain the species of forest undergrowth, the respective frequency values for individual tree canopy species within the considered associations could be found elsewhere (see ZLATNÍK 1935: 99, 112–113, 116–117) as for example BRAUN-BLANQUET ET AL. (1939: 28: values for *Picea abies*) did. Probably the only possible way to finish the solution of the nomenclatural issue concerning the original association names of ZLATNÍK (1935) is to ask for a binding decision following the regulations of the new Code edition (THEURILLAT ET AL. 2021).

Norway spruce phytocoenoses were excluded from *Bazzanio-Piceetum* in the most recent Austrian woodland vegetation survey (cf. EXNER 2007).

However, already SCHMID & GAISBERG (1936) (see also OBERDORFER 1938, BARTSCH & BARTSCH 1940) reminded of important anthropogenically induced changes of these communities. The long-term artificial predominance of Norway spruce considerably unified the appearance of the field layer flora (cf. BRAUN-BLANQUET et al. 1939: 33) and supported secondary expansion of the ground layer species as well as their total cover. Thus, the primary floristical differences between different vegetation types mostly disappeared (see relevés of SCHMID & GAISBERG 1936, tab. III). Modern geobotanical knowledge on anthropogenic changes of the Northern Black Forest vegetation was summarized by MURMANN-KRISTEN (1987) who explicitly labelled the original diagnosis of *Luzulo luzuloidis-Piceetum* as ‘woodland-artificial forest hybrid’. However, the original relevés of SCHMID & GAISBERG (1936) separated by BRAUN-BLANQUET et al. (1939) into the *Bazzanio trilobatae-Piceetum* (ut *Mastigobryo-Piceetum*) also represent succession stages of anthropogenic phytocoenoses, partially on formerly deforested habitats.

(A1) Within the *Luzulo-Piceetum* (= *Piceetum normale* of SCHMID & GAISBERG [1936]), the ‘*Luzula sylvatica* facies’ represents a degraded, substitutionary *Picea* version of distinct *Luzula sylvatica*-rich montane mixed *Abies-Fagus-Picea* woodland (cf. OBERDORFER 1938, tab. 24, rel. 8; BARTSCH & BARTSCH 1940, tab. 21, rels. 10–12) somewhat related to *Aceri-Fagetum* Bartsch et Bartsch ex Trautmann 1952 (incl. *Fago-Piceetum adenostyletosum albifrontis* Oberdorfer 1938 nom. incept.).<sup>39</sup> The former community was later classified as *Luzulo luzuloidis-Abietetum luzuletosum sylvaticae* Oberdorfer 1957 or, respectively, *Adenostylo-Piceetum* Hartmann 1953 (see below). It might constitute a *Luzulo-Fagetalia* equivalent to *Acero-Fagetum*.

(A2+3) Both *Luzulo-Piceetum* facies *Oxalis-Myrtillus* and *Luzula luzuloides-Myrtillus* of SCHMID & GAISBERG (1936) represent the nomenclaturally typical form of the association and at the same time degraded (see also MURMANN-KRISTEN 1987) montane *Luzulo-Fagetalia* communities (cf. the occurrences of *Carex pilulifera* and *Agrostis* sp.).

The later published association *Luzulo luzuloidis-Abietetum* Oberdorfer 1957<sup>40</sup> is for the most part syntaxonomically synonymous to *Luzulo luzuloidis-Piceetum* (Schmid et Gaisberg 1936) Br.-Bl. et Sissingh in Br.-Bl. et al. 1939 nom. corr. and, at the same time, they both are closely related to the slightly species-richer association *Galio rotundifolii-Piceetum* J. Bartsch & M. Bartsch 1940 (see BARTSCH & BARTSCH 1940, tab. 21) with *Ajuga reptans*, *Anemone nemorosa*, *Galium rotundifolium* and *Paris quadrifolia*.

(B1+2) Equivalently, the original diagnoses of the facies *Myrtillus-Hylocomium* and *Myrtillus-Hylocomium-Sphagnum* within the subassociation *Bazzanio-Piceetum myrtilletosum* (Schmid et Gaisberg 1936) Br.-Bl. et Sissingh in Br.-Bl. et al. 1939<sup>41</sup> (Art. 14b) represent an impoverished version of the previously mentioned association *Luzulo luzuloidis-Piceetum*, i.e.

<sup>39</sup> A possible older publication of this name should be searched. Alternatively, the long time accepted name ‘*Aceri-Fagetum* Bartsch & Bartsch 1940’ should be proposed as nomen conservandum in respect of nomenclatural stability (cf. KUČERA 2013a; cf. THEURILLAT et al. 2021).

<sup>40</sup> This widely accepted and long-term used syntaxonomic name should probably be proposed for conservation against *Luzulo luzuloidis-Piceetum* (Schmid et Gaisberg 1936) Br.-Bl. et Sissingh in Br.-Bl. et al. 1939 nom. corr.

<sup>41</sup> This name would hypothetically constitute the autonym *Bazzanio-Piceetum typicum* (Art. 13b) according to lectotypification by KUČERA (2010a: 834); however, see below.

even more degraded lower montane *Luzulo-Fagetalia* phytocoenoses; however, some habitats could also naturally promote a higher abundance of *Picea*. Already SCHMID & GAISBERG (1936) reminded of the artificial character of this forest community and the higher abundance of *Abies* in the surveyed forests (outside of their relevé plots) and the same could be expected for the potential natural distribution of *Fagus* (see MURMANN-KRISTEN 1987).

In respect of an earlier lectotypification (KUČERA 2010a) and contrary to my previous statement (KUČERA 2009a), these two *Bazzanio-Piceetum myrtilletosum* types represent probably more humid variants of the subassociation *Fago-Piceetum vaccinietosum* Oberdorfer 1938 s. str. from the syntaxonomical point of view. Therefore, they should be united under the association name *Fago-Piceetum* Oberdorfer 1938 (syntax. syn.: *Vaccinio myrtilli-Abietetum* Zeidler 1953; non: *Myrtillo-Abietetum* Kuoch 1954 nom. illeg. [Art. 14b, 31], *Bazzanio-Abietetum* (Meyer 1949) Ellenberg et Klötzli 1974). Both names of ZEIDLER (1953) and OBERDORFER (1938) represent phytocoenologically very similar species-poor, anthropogenic mixed *Abies* forest communities, thus Oberdorfer's association name *Fago-Piceetum* is probably the oldest validly published name for this syntaxon.

(B3) The phytocoenoses of *Myrtillus-Aspidium* (*Dryopteris carthusiana*)<sup>42</sup> facies of the *Bazzanio-Piceetum myrtilletosum* (SCHMID & GAISBERG 1936, tab. III) were recorded on ± steep and scree habitat types. Irrespective of their purposive *Picea*-biased character (see above), they should represent a slightly more natural community with originally more abundant *Abies alba* – cf. Silver fir abundances within the ecologically even more extreme habitats of *Sphagno quinquefarii-Abietetum* Chipon et al. ex Cartier et al. in Boeuf et al. 2014 (BOEUF et al. 2014). They form an ecologically ± analogous community to *Luzulo luzuloidis-Abietetum luzuletosum sylvaticae* (see above), but they occupy nutrient-poorer and more soil skeleton-rich habitats. BARTSCH & BARTSCH (1940, tab. 20) recorded partly the same community; however, partially with anthropogenic occurrence of *Molinia caerulea* (see below). Their *Bazzanio-Piceetum* relevés were later included by OBERDORFER (1957) into the subassociation '*Bazzanio-Piceetum typicum*' specifically including the *Bazzania* scree phytocoenoses (see below).

Similar scree slope habitats with dominant *D. dilatata* are in the higher elevations of the Sudetes and the Western Carpathians occupied by woodland stands of the association *Dryopterido dilatatae-Piceetum* Sýkora ex Jirásek 1996 which is, in contrast, considered for true natural *Piceion abietis* community according to current knowledge (JIRÁSEK 2002; cf. KUČERA in red.).

(C1–3) According to SCHMID & GAISBERG (1936), the stands of subassociation *Bazzanio-Piceetum vaccinietosum vitis-idaeae* (Schmid et Gaisberg 1936) Br.-Bl. et Sissingh in Br.-Bl. et al. 1939 (Rec. 10C vs. the previous name *Bazzanio-Piceetum myrtilletosum* (Schmid et Gaisberg 1936) Br.-Bl. et Sissingh in Br.-Bl. et al. 1939) – especially the facies *Vaccinium-Hylocomium-Sphagnum* and *Vaccinium-Hylocomium* – should represent the actual forest vegetation of higher elevations of the Northern Black Forest. Their original relevés still indicate a mixed *Abies* and *Picea* woodland and Schmid and Gaisberg properly recognized the artificial character of almost pure Norway spruce stands commonly found in the considered altitudinal zone.

However, the existence of a supramontane natural Norway spruce altitudinal zone is not expected within the Northern Black Forest (see BARTSCH & BARTSCH 1940 vs. MURMANN-KRISTEN

<sup>42</sup> Most of the records of *Dryopteris carthusiana* of Schmid & Gaisberg (1963, tab. III) may, in fact, represent *D. dilata* (cf. OBERDORFER 1938, tabs. 24, 25; BARTSCH & BARTSCH 1940, tab. 20, 21; MURMANN-KRISTEN 1987).

1987 and there cited literature). Records of *Abies alba* high cover-abundance values confirm the substantial vitality of this tree species also in the higher elevations of the Northern Black Forest (BARTSCH & BARTSCH 1940, MURMANN-KRISTEN 1987). In this respect, further field studies should be performed to determine the potential natural abundance of *Abies* (as well as *Fagus*) in the highest vegetation zone of the Northern Black Forest as well as to solve the disputable question of their syntaxonomical classification (among very acid and species-poor upper montane *Luzulo-Fagetalia* syntaxa or, less probably, *Piceetalia abietis* syntaxa).

In addition, the almost constant presence of *Molinia caerulea* within the *Bazzanio-Piceetum vaccinietosum vitis-idaeae* published by SCHMID & GAISBERG (1936, tab. III), partially by both BARTSCH & BARTSCH (1940, tab. 20) and OBERDORFER (1938, tab. 25) indicate strong anthropogenic influence on the respective habitats: following SCHMID & GAISBERG (1936), it should be reminded that past deforestation contributes to secondary expansion of *Molinia*. MURMANN-KRISTEN (1987) explicitly includes *M. caerulea* in the group of indicators of former pasture management within the Northern Black Forest, together with *Pteridium aquilinum* and partially *Galium saxatile* and *Sphagnum capillifolium*. Thus, especially relevés published by Schmid and Gaisberg represent stages of spontaneous woodland secondary succession, probably mostly on historical totally deforested areas.

(C1) In respect of the preceding *Bazzanio-Piceetum* lectotypifications (KUČERA 2010a), the forest facies *Vaccinium-Hylocomium-Sphagnum* described by SCHMID & GAISBERG (1936) and later transferred into *Bazzanio-Piceetum vaccinietosum vitis-idaeae* (BRAUN-BLANQUET et al. 1939) should be considered as ecologically and phytocoenologically distinct syntaxon. In regard to considerable floristical similarity to the community described by KUOCH (1954) as '*Myrtillo-Abietetum* Kuoch 1954 *Bazzania*-variant', the considered unit should be included into *Myrtillo-Abietetum*.

However, considering the nomenclatural and syntaxonomical circumstances, this syntaxon is here differentiated within the association *Lycopodio annotini-Abietetum* Thébaud 2008<sup>43</sup> (syntax. syn. *Myrtillo-Abietetum* Kuoch 1954<sup>44</sup> nom. illeg.; non: *Lycopodio-Abietetum* Fajmonová 1974 ass. prov. [Art. 3b]) as the following subassociation:

*Lycopodio annotini-Abietetum albae vaccinietosum vitis-idaeae* (Schmid et Gaisberg 1936)  
P. Kučera comb. nov. hoc loco (basionym: *Piceetum vaccinietosum* Schmid et Gaisberg 1936 s. str. (as delimited by its lectotypification), SCHMID & GAISBERG (1936), tab. III; nomenclatural type: KUČERA 2010a: 834).

Considering the variability of the here accepted concept of the association *Lycopodio annotini-Abietetum* Thébaud 2008, following subassociations are further differentiated:

– *Lycopodio annotini-Abietetum typicum* subass. nov. hoc loco (Art. 26) (≡ *Lycopodio annotini-Abietetum* Thébaud 2008 s. str. – original diagnosis: THÉBAUD (2008: 86), tab. 1, relevés of the column A; nomenclatural type: THÉBAUD [2008: 77], holotype),

<sup>43</sup> THÉBAUD (2008) lists species including *Blechnum spicant*, *Lycopodium annotinum*, *Plagiothecium undulatum*, *Ptilium crista-castrum*, *Rhytidadelphus triquetrus* as differential taxa against *Myrtillo-Abietetum* Kuoch 1954 nom. illeg. (Art. 31, to *Vaccinio myrtilli-Abietetum* Zeidler 1953; cf. Art. 14b – without the correction of the Kuoch's name form). However, the original diagnosis of the latter association proves their presence also in *Myrtillo-Abietetum*. For this reason, these two syntaxa are here united into one association with several subunits.

<sup>44</sup> Lectotypification THÉBAUD (2008: 76).

- Lycopodio annotini-Abietetum bazzanietosum trilobatae* P. Kučera subass. nov. hoc loco (original diagnosis: *Myrtillo-Abietetum* Kuoch 1954 *Pleuroschisma*-Variante, KUOCH (1954), tab. 7, rels. 34–46; nomenclatural type: KUOCH (1954), tab. 7, rel. 41).
- Lycopodio annotini-Abietetum avenelletosum flexuosae* (Thébaud 2008) P. Kučera comb. nov. hoc loco (basionym: *Myrtillo-Abietetum avenelletosum flexuosae* Thébaud 2008, THÉBAUD (2008: 76); nomenclatural type: THÉBAUD [2008: 76]).
- Lycopodio annotini-Abietetum mycelidetosum muralis* (Thébaud 2008) P. Kučera comb. nov. hoc loco (Art. 26, 44) (basionym: *Myrtillo-Abietetum typicum* differentiated by THÉBAUD (2008: 76); original diagnosis: *Myrtillo-Abietetum* Kuoch 1954 *typische*-Variante, KUOCH (1954), tab. 7, rels. 19–33;<sup>45</sup> nomenclatural type: THÉBAUD [2008: 76]; the name-giving taxon *Mycelis muralis* is given by KUOCH (1954) under the older synonym ‘*Cicerbita muralis* (L.) Wallroth (*Lactuca*)’).

(C2) The second original subcommunity of the *Bazzanio-Piceetum vaccinietosum vitis-idaeae* – the *Vaccinium-Hylocomium* facies Schmid & Gaisberg (1936) – was mostly recorded on steeper slopes of the higher elevations of the Northern Black Forest and the relevés represent mostly substitutionary *Picea* phytocoenoses according to the original authors. More detailed field examination should clear the syntaxonomical position of this subcommunity, either within *Bazzanio-Piceetum* sensu Oberdorfer 1957 or *Lycopodio annotini-Abietetum* or *Sphagno quinquefarii-Abietetum*.

(C3) The third, *Vaccinium-Sphagnum* facies of *Bazzanio-Piceetum vaccinietosum vitis-idaeae* of SCHMID & GAISBERG (1936) (cf. ‘*Bazzanio-Piceetum vaccinietosum uliginosi*’ Seibert 1992) demonstrates development of a waterlogged habitat; however, the species diversity and abundances are anthropogenically influenced by past deforestations and other indirect influences as well (*Molinia caerulea*, *Pteridium aquilinum*). Nevertheless, the presence of *Empetrum nigrum* and *Vaccinium uliginosum* in the smaller part of relevés indicate that the respective original relevés of SCHMID & GAISBERG (1936) represent a distinct waterlogged community.

Considering the anthropogenic influence on the phytocoenoses included by SCHMID & GAISBERG (1936) into the *Vaccinium-Sphagnum* facies, the original relevés should be syntaxonomically revised and divided: probably into *Lycopodio annotini-Abietetum albae vaccinietosum vitis-idaeae*, *Lycopodio annotini-Abietetum bazzanietosum trilobatae* and *Soldanello-Piceetum* (see above) and, marginally, *Vaccinio uliginosi-Pinetalia*.

Less biased relevés were published by DIERSSEN & DIERSSEN (1984, tab. 25); however, their records represent two different communities:

- the relevés 1–8 belong to the order *Sphagno-Piceetalia* P. Kučera 2019 and they are close to the association *Soldanello montanae-Piceetum* Volk in Br.-Bl. et al. 1939 (cf. subassociations *bazzanietosum trilobatae* and *caricetosum nigrae*; KUČERA 2019b and KUČERA in red.); for comparison the original diagnosis of the association *Bazzanio-Abietetum* (Meyer 1949) Ellenberg et Klötzli 1974 is also available (basionym: *Mastigobryeto-Piceetum abietetosum* Meyer 1949; cf. MEYER 1949 vs. ELLENBERG & KLÖTZLI 1972: 46; incl. *Rhytidiadelpho lorei-Abietetum albae typicum* Frehner ex Boeuf in Boeuf et al. 2014; cf. BOEUF et al. 2014) described for phytocoenoses of the lower altitudes;

<sup>45</sup> Species-rich relevés separated by KUOCH (1954, tab. 7, rels. 1–18) to the community ‘*Myrtillo-Abietetum* Kuoch 1954 *Lysimachia*-Variante’ floristically and ecologically do not belong to the association *Lycopodio annotini-Abietetum* Thébaud 2008 (cf. also THÉBAUD 2008: 77).

—on the contrary, the relevés 9–22 with constant presence of *Vaccinium uliginosum*, *Sphagnum angustifolium*, *S. magellanicum* belong to the order *Vaccinio uliginosi-Pinetalia* Passarge 1968 (cf. WILLNER & STEINER 2007).

Similarly, MURMANN-KRISTEN (1987) published records of *Bazzanio-Piceetum* as well, differentiated into two subassociations *sphagnetosum* and *typicum*. However, the relevés come from floristically and ecologically different habitats, including: (1) waterlogged wetlands on flat relief (cf. *Soldanello-Piceetum*), (2) *Bazzania*-rich woodland of steeper slopes, partially with abundant selected *Sphagnum* species (? *Bazzanio-Piceetum typicum* sensu Oberdorfer 1957) and (3) a *Vaccinio uliginosi-Pinetalia* mire habitat (rel. 11).

(C, final notes) As explained above, the specific approach of SCHMID & GAISBERG (1936) to the selection of recorded relevé plots (mainly phytocoenoses with *Picea abies* dominance) was not reflected by most of the later scientists. At the same time, the great number of various later syntaxonomical applications of the association *Bazzanio-Piceetum* did not correspond to more or less any part of the original diagnosis of *Bazzanio-Piceetum* s. str. (i.e. as determined by SCHMID & GAISBERG 1936). Therefore, although the relevant lectotypifications proposed by KUČERA (2010a: 834) were made in effort to focus on the original character of the community as recorded by SCHMID & GAISBERG (1936), they would represent a substitutionary *Picea* forest community and not the application as semi-natural community as presented, for example, by OBERDORFER (1957) and SEIBERT (1992).

In spite of that, the name *Bazzanio trilobatae-Piceetum* (Schmid et Gaisberg 1936) Br.-Bl. et Sissingh in Br.-Bl. et al. 1939 belong to a group of long-accepted and widely known syntaxa names in botanical science. Therefore, conservation of the name application should be considered, especially in the view of the best advantage of the potential use for a ± semi-natural community and at the same time close to *Bazzanio trilobatae-Piceetum* original diagnosis published by SCHMID & GAISBERG (1936).

However, to prevent the possibility that the names *Soldanello montanae-Piceetum* Volk in Br.-Bl. et al. 1939 and *Bazzanio trilobatae-Piceetum* would become syntaxonomical synonyms – as wetland more or less *Sphagnum*-rich communities of the order *Sphagno-Piceetalia* (cf. KUČERA 2019b: *Soldanello-Piceetum*); see, for example, DIERSSEN & DIERSSEN (1984) and MURMANN-KRISTEN (1987) – the appropriate syntaxonomical delimitation of the association *Bazzanio trilobatae-Piceetum* could be extracted from the relevés included by OBERDORFER (1957: 378) to the subassociation ‘*Bazzanio trilobatae-Piceetum typicum*’; however, with exclusion of mire communities and thus with specific focus on ± scree *Bazzania trilobata*-phytocoenoses (cf. SCHMID & GAISBERG 1936, tab. III, *Myrtillus-Aspidium* facies and also SEIBERT 1992). Therefore, a new conserved nomenclatural type is proposed here following Oberdorfer’s selection of *Bazzanio-Piceetum typicum* relevés:

*Bazzanio trilobatae-Piceetum* (Schmid et Gaisberg 1936) Br.-Bl. et Sissingh in Br.-Bl. et al. 1939 nom. corr. et typus cons. propos. hoc loco

Nomenclatural type: BARTSCH & BARTSCH (1940), tab. 20, rel. 2, lectotypus conservandum hoc loco (cf. also BARTSCH & BARTSCH (1940), tab. 20, rel. 6).

(IV) The association *Adenostylo-Piceetum* Hartmann 1953 was commonly accepted to represent a synonym to the association *Athyrio distentifolii-Piceetum* Hartmann ex Hartmann et Jahn 1967

(see above the nomenclatural note to *Athyrio distentifolii-Piceetum*). However, the former name is based on relevés of the community '*Luzulo luzuloidis-Piceetum* (Schmid et Gaisberg 1936) Br.-Bl. et Sissingh in Br.-Bl. et al. 1939 *Luzula sylvatica*-Fazies' (BARTSCH & BARTSCH 1940, tab. 21, rels. 10–12) which features anthropogenically influenced mixed montane woodland of the class *Carpino-Fagetea*, originally with higher abundance of *Fagus sylvatica* (KUČERA 2012a: 239–240).

(V) The association *Luzulo sylvaticae-Piceetum* (Wraber ex) Wraber 1963 is commonly considered to represent a natural *Picea abies* woodland of the alliance *Piceion abietis* and its distribution is – except of Slovenia – suggested from Ukraine and by some authors within Austria and Romania (WRABER 1955; ZUPANČIČ 1999; ŠILC & ČARNI 2012; JUVAN et al. 2013; Dubyna et al. 2019; cf. WALLNÖFER 1993 vs. EXNER 2007; CHIFU 2014 vs. COLDEA 2015). However, the only key to the appropriate interpretation of any syntaxon (THEURILLAT et al. 2021) is the original diagnosis provided within the first valid publication of the respective name (and placed in a broader context): in this case the original relevé data of *Luzulo sylvaticae-Piceetum* published by WRABER (1963, tab. 1), mostly from the Pohorje Mts, a north Slovenian mountain range.

Already WRABER (1963) highlighted the fact that *Fagus sylvatica* has substantial abundance within the considered forest type (almost 60% in the tree layer of 54 published relevés, half of the occurrences with cover-abundances 2 to 5, locally in co-dominance with *Picea* at the altitude of 1400 m a.s.l. on the north-west slope, abundant even at 1450 m a.s.l.) and that the long-term land management has markedly negative impact on the natural distribution of *Fagus* as well as of *Abies alba*. On the contrary, existence of pure *Picea* stands was explained by impacts of applied land management by WRABER (1955). Nevertheless, the highest-most localities of low-growth *Fagus* trees were noted by WRABER (1956, 1963) even at ca. 1520–1530 m a.s.l. In addition, WRABER (1963: 104) included to his *Luzulo sylvaticae-Piceetum* even selected pure *Fagus* stands of high altitudes of the Pohorje Mts.

However, the most important phytocoenological feature is the pattern of the floristical variability of the original diagnosis of *Luzulo sylvaticae-Piceetum*. Although the relevés of the Wraber's subassociations reliably represent various ecological habitat types, they are considerably uniform – the only exception is the distinct habitat-specific subassociation *Sphagnetosum acutifolii*. This fact means that approximately the same vegetation composition within the individual subassociations is developed irrespectively to (historically recorded) *Picea/Abies/Fagus* abundances. Additional original relevés published by ZUPANČIČ (1999) show a similar vegetation type. As mixed *Fagus* woodlands are generally not classified within the class of natural *Picea abies* communities (*Vaccinio-Piceetea*) in the present, an other explanation for the vegetation type recorded by WRABER (1963) is needed.

Wraber thoroughly studied the vegetation of Pohorje Mts and, among others, differentiated a distinct upper montane mixed *Fagus* community which was later named *Aceri-Fagetum pohoricum* (WRABER 1953, 1954, 1955, 1956, 1963) – the corresponding name was formally validated by ZUPANČIČ (1969). However, the development of this community was supposed by WRABER (1963) only locally under 'more favorable habitat conditions within the Norway spruce vegetation zone', up to 1400–1450 m a.s.l.. and the other type of more or less pure *Fagus* phytocoenoses was classified by Wraber into *Luzulo sylvaticae-Piceetum* (WRABER 1963: 157).

However, *Fagus* phytocoenoses are not classified within *Vaccinio-Piceetea* communities (i.e. natural *Picea abies* woodlands) in compliance to modern phytocoenological approaches as they

belong to *Carpino-Fagetea* syntaxa, at the same time the existence of multiple *Fagus* stands indicate affiliation of such habitats to upper montane vegetation and not to the supramontane zone.

During my visit to Slovenia, existence of (close to natural) *Fagus* woodland islands above 1420–1430 m a.s.l. in the Pohorje Mts. was confirmed on SE and NEN slope orientation eastwards of Jezerski vrh Mt. (1537 m a.s.l.) (e.g. 46°29'25" N, 15°16'35" E, ca. 1435 m a.s.l., 8.11.2013, P. Kučera, not.). The most conspicuous observed vegetation feature is a more or less very sharp vegetation boundary separating spatially directly adjacent pure *Fagus* and pure *Picea* phytocoenoses inhabiting the same ecological habitat. In addition, remnants of mountain pastures are present here and there indicating that the distribution of these *Fagus* stands was anthropogenically reduced (see also WRABER 1954). Symptomatic are not only more or less horizontal but also sharp vertical borders of such *Fagus* stands or islands (from above and even from below).

Significant anthropogenic impact is further illustrated by occurrences of *Nardus stricta*, *Potentilla erecta*, *Veronica officinalis*, (partially also *Deschampsia cespitosa*), *Hypericum maculatum* and even *H. perforatum* which indicate former influence of mountain pasture or, alternatively, historical deforestation of the respective relevé localities of WRABER (1963). Moreover, Wraber's records of species including *Polygonatum verticillatum*, *Senecio ovatus*, *Anemone nemorosa*, *Galeobdolon luteum*, *Knautia drymeia*, *Silene dioica* or *Phyteuma spicatum* indicate the rather upper montane mixed *Carpino-Fagetea* community than true natural acid Norway spruce community, represented in the regions of most Central European mittelgebirge mountain ranges built by silicate rocks most frequently by the association *Lophozio-Piceetum*.

Long-term stability of the tree layer species composition, i.e. permanent dominance of *Fagus* without significant traces of re-establishment of *Picea*-dominated mixed stands, contradicts to hypothesis of WRABER (1963: 157) that such *Fagus* islands represent the result of selective tree harvesting. On the contrary, the secondary succession of *Fagus* within adjacent *Picea* stands is progressively developed – depending only on the amount of preserved (or previously recolonised) *Fagus* trees in the surroundings. Such processes indicate spontaneous re-establishment of natural mixed *Fagus* woodland of the upper montane vegetation zone.

The same stability and *Fagus* secondary succession was observed in the Western Carpathian mountain ranges (KUČERA 2012a, 2013a, 2014, 2015), although in lower altitudes due to more northern latitude (around 1350–1370–1400 m a.s.l.). It should be noted, that the respective vegetation changes should not be assigned only to climate change as its impact to the respective anthropogenic spreading of *Fagus* should be expected mainly within the potential natural altitudinal zone of *Picea* woodlands as reconstructed for the period 1950–1980.

Another feature similar to surveyed Western Carpathian forest stands is that secondary *Picea abies* stands anthropogenically substituting the original mixed *Fagus* stands and bordering preserved *Fagus* woodland islands have frequently considerably changed the vegetation cover of the undergrowth layers. Long-term, yet temporary, dominance of *Picea* supported significantly increased ground layer cover as well as abundances of bryophyte species and at the same time subanthropogenic expansion of *Vaccinium myrtillus*, *V. vitis-idaea*, *Homogyne alpina*, partially also *Luzula sylvatica*. During spontaneous reverse succession of *Fagus* described above, these temporary vegetation changes disappear; however, this process would last more decades in high altitudes, where mixed *Fagus* woodlands were mostly destroyed.

Within the Pohorje Mts, multiple occurrences of high elevation *Fagus* stands, continuous woodlands or anthropogenically restricted islands could be found. as it can be seen from the maps provided by ‘The Surveying and Mapping Authority of the Republic of Slovenia’ (<http://www.geoportal.gov.si/eng/viewers/>), e.g. on the slopes of Mala kopa Mt. (1524 m), Otiše Mt. (1416 m), Črni vrh Mt. (1543 m), Jezerski vrh Mt. (1537 m), Javorič (1430 m). The evidence of *Fagus* woodland occurrences around 1400 m a.s.l. (and higher) is most important also in northwardly oriented habitats. Together, they indicate that the upper montane altitudinal vegetation zone, originally occupied by mixed *Fagus* woodland, reached probably ca. 1460–1500 m a.s.l. in the Pohorje Mts and, equivalently, in other non-carbonate mountain ranges of non-dinaric mittelgebirge character. The statement of WRABER (1963) that the altitudinal zone from 1250–1300 m a.s.l. is generally taken by *Luzulo sylvaticae-Piceetum* as a natural Norway spruce community is questionable.

The opinion of WRABER (1963) that *Luzulo sylvaticae-Piceetum* represents for the most part a degraded *Carpino-Fagetea* phytocoenoses is further supported by soil types developed under *Luzulo sylvaticae-Piceetum*: according to WRABER (1963) frequently cambisols are developed under stands which he classified within the *Luzulo sylvaticae-Piceetum* while, on the contrary, podzols are characteristic of the altitudinal zone of natural Norway spruce communities.

The observed vegetation and ecological pattern indicate that the original relevé data of the association *Luzulo sylvaticae-Piceetum* published by WRABER (1963) represent for the most part significantly anthropogenically modified phytocoenoses of the former natural mixed *Fagus* communities, and as such they have to be classified within the class *Carpino-Fagetea* (see above the related syntaxonomical comments within the individual subchapters on acid Norway spruce communities in Slovakia and KUČERA 2022). Consequently, the below presented typifications aim to adjust application of the considered syntaxa to phytocoenological character recorded by WRABER (1963).

In this sense, we also have to interpret the high proportion of *Fagus* and *Abies* (58%) in the group of natural ‘acidophilous high elevation spruce, larch and fir forests’ (i.e. including relevés from the Pohorje Mts.) within the Slovenian relevé dataset evaluated by JUVAN et al. (2013). It is possible that a significant number of the relevés supposed to represent natural Norway spruce communities come from substitutionary *Picea* variants of *Carpino-Fagetea* communities (cf. above Table 1 and KUČERA 2022).

(VI) The association *Calamagrostio villosae-Piceetum* Schlüter 1966 originally described from the Thuringian Forest (eastern central Germany) was brought into use to replace the younger homonymous name *Calamagrostio villosae-Piceetum* Hartmann et Jahn 1967 nom. illeg. (Art. 31). However, the oldest validly published name corresponding to the latter name is *Lophozio-Piceetum* Volk in Braun-Blanquet et al. 1939 (KUČERA 2012a).

The name *Calamagrostio villosae-Piceetum* Schlüter 1966 was proposed by Chytrý (in CHYTRÝ et al. 2013b: 406) as nomen conservandum against *Lophozio-Piceetum* Volk in Braun-Blanquet et al. 1939 and *Sphagno-Piceetum* (Tüxen 1937) Hartmann 1953. However, the two latter names represent syntaxonomically different communities in comparison to anthropogenically induced substitutionary forest stands of the original diagnosis of *Calamagrostio villosae-Piceetum* Schlüter

1966 (see also above notes within the subchapter *Lophozio-Piceetum* and KUČERA 2019b). Therefore, the considered nomenclatural proposal is redundant.

(VII) Careful consideration is necessary also in the case of the original phytocoenoses included by HARTMANN & JAHN (1967) in their validly described associations *Calamagrostio villosae-Piceetum Hartmann et Jahn 1967 nom. illeg.* (Art. 31) as well as *Athyrio distentifolii-Piceetum Hartmann ex Hartmann et Jahn 1967*. In comparison to natural *Picea* woodlands of the Western Carpathian mittelgebirge mountain ranges, the original relevés published by HARTMANN & JAHN (1967, tabs. 1, 2) contain significant number of species occurrences including *Blechnum spicant*, *Calamagrostis arundinacea*, *Galium saxatile*, *Streptopus amplexifolius*, *Trientalis europaea* and especially *Polygonatum verticillatum*.

The first explanation is that their frequencies might represent a phytochorological variant of natural *Picea abies* phytocoenoses within the parallel Hercynian mittelgebirge mountain ranges.

However, in my opinion a more probable interpretation is that the supposedly natural *Picea* forest stands having higher frequency of these species (except of *Trientalis*) within the considered relevés published by HARTMANN & JAHN (1967) represent, in fact, mostly sub-/anthropogenic stands of degraded *Carpino-Fagetea* communities, developed under the impacts of long-term land management which caused a considerable species change of the original mixed *Carpino-Fagetea* phytocoenoses and a modification of habitat conditions (see above comments to *Athyrio distentifolii-Piceetum athyrietosum filicis-feminae* Hartmann et Jahn 1967 with regard to the revision of the natural distribution of *Picea abies* woodlands in the Western Carpathians [KUČERA 2012a]). This view is supported by MURMANN-KRISTEN (1987: 92) in case of *Polygonatum verticillatum* (in case of upper montane acid mixed *Fagus* woodlands); however, see also *Blechnum spicant*, *Bazzania trilobata* (MURMANN-KRISTEN 1987, tab. 7, 8).

Evidences of ± similar occurrence patterns of these species from the Hercynian region within supposedly natural *Picea abies* (or in broader sense coniferous) woodlands were published by MATUSZKIEWICZ & MATUSZKIEWICZ (1960); SAMEK (1961); DUNZENDORFER (1974); MATUSZKIEWICZ (1977); SOFRON (1981); NEUHÄUSLOVÁ & ELTSOVA (2003); EWALD et al. (2011); cf. also CHYTRÝ et al. (2013b). This fact indicates the increased possibility that field revision of the natural distribution *Picea abies* woodlands is needed also in European countries other than Slovakia (including Carpathian part of Moravia and Silesia; cf. subchapters *Lophozio-Piceetum* and *Athyrio distentifolii-Piceetum*). Although *Blechnum*, *Calamagrostis arundinacea*, *Polygonatum verticillatum*, *Streptopus* etc. undoubtedly belong to montane species (*sensu lato*) in acid habitats of Central European mittelgebirge mountain ranges, they may be typical of upper montane mixed *Fagus* woodlands (*Carpino-Fageta*) and, as a general rule, they also indicate their anthropogenic *Picea* variants (cf. OBERDORFER 1938; SCHMID & GAISBERG 1936; BARTSCH & BARTSCH 1940) instead of being character-species for supramontane *Picea* woodlands (*Vaccinio-Piceetea*) in Central Europe (cf. MIKYŠKA 1972; DUNZENDORFER 1974; PETERMANN et al. 1979; NEUHÄUSLOVÁ & SOFRON 2005; EWALD et al. 2011; Hédl in BOUBLÍK et al. 2013 [*Calamagrostio villosae-Fagetum*] vs. CHYTRÝ et al. 2013b). Their distribution in true natural Norway spruce communities of Central European mittelgebirge mountain ranges within the alliance *Piceion abietis* is rather sporadic or, in selected cases, limited to special habitats (see above). In any case they should not be considered as Braun-Blanquetian character species of the alliance *Piceion abietis* (or the class *Vaccinio-Piceetea*).

## 5. Nomenclatural and syntaxonomical supplement

As indicated above, the phytocoenological application of the association *Luzulo sylvaticae-Piceetum* Wraber 1963 frequently differs from the floristical and ecological content of the original diagnosis of this unit. Therefore, following lectotypifications are proposed to consolidate the use of the respective syntaxa in accordance with their phytocoenotic content defined by the relevés of WRABER (1963):

- *Luzulo sylvaticae-Piceetum* Wraber 1963 – nomenclatural type: WRABER (1963), tab. 1, rel. 18, lectotypus hoc loco.
- *Luzulo sylvaticae-Piceetum sphagnetosum capillifolii* Wraber 1963 nom. corr. (Art. 44) (original name: *Luzulo sylvaticae-Piceetum sphagnetosum acutifolii* Wraber 1963 nom. inept.; Rec. 10C) – nomenclatural type: WRABER (1963), tab. 1, rel. 4,<sup>46</sup> lectotypus hoc loco. Syntaxonomical and ecological relation to *Soldanello montanae-Piceetum homogynetosum alpinæ* (Trautmann 1952) P. Kučera 2019 (order *Sphagno palustris-Piceetalia*) should be studied in more detail.
- *Luzulo sylvaticae-Piceetum rhytidiaadelphetosum lorei* Wraber 1963 (Art. 14b) – nomenclatural type: WRABER (1963), tab. 1, rel. 5,<sup>47</sup> lectotypus hoc loco.
- *Luzulo sylvaticae-Piceetum typicum* (≡ *Luzulo sylvaticae-Piceetum typicum* Wraber 1963) – nomenclatural type: WRABER (1963), tab. 1, rel. 18, automatical lectotype (Art. 5b). Regardless of the altitudes of the individual original stand, stands of this subassociation typically represent impoverished version of phytocoenoses of the *Luzulo sylvaticae-Piceetum fagetosum* (still preserved are *Galeobdolon lutetum*, *Polygonatum verticillatum*, *Athyrium filix-femina*, *Phyteuma spicatum* etc.), while secondary more abundant *Picea* supported expansion of *Calamagrostis villosa* and bryophytes' occurrence in higher number (even presence of lichens); see also reclassification of Wraber's original relevés by ZUPANČIČ (1999, tab. 6) to other subunits.
- *Luzulo sylvaticae-Piceetum avenelletosum flexuosae* Wraber 1963 nom. corr. (Art. 44) (original name: *Luzulo sylvaticae-Piceetum deschampsietosum flexuosae* Wraber 1963 nom. inept.) – nomenclatural type: WRABER (1963), tab. 1, rel. 36, lectotypus hoc loco. This community represents probably a species-poor *Luzulo-Fagetalia* syntaxon.
- *Luzulo sylvaticae-Piceetum fagetosum sylvaticae* Wraber 1963 – nomenclatural type: WRABER (1963), tab. 1, rel. 42, lectotypus hoc loco.
- *Luzulo sylvaticae-Piceetum calamagrostietosum arundinaceae* Wraber 1963 – nomenclatural type: WRABER (1963), tab. 1, rel. 47, lectotypus hoc loco. As specified by WRABER (1963), this community is developed in a more steep habitat and probably represents a separate community, cf. *Aceri-Fagetum calamagrostietosum arundinaceae* as defined by BARTSCH & BARTSCH (1940).
- *Luzulo sylvaticae-Piceetum doronicetosum austriaci* Wraber 1963 – nomenclatural type: WRABER (1963), tab. 1, rel. 54, lectotypus hoc loco; paralell to *Aceri-Fagetum adenostyletosum alliariae* as defined by BARTSCH & BARTSCH (1940)?

<sup>46</sup> I.e. not from the *Carex brizoides*-variant of WRABER (1963: 112–114), cf. *Luzulo sylvaticae-Piceetum caricetosum brizoidis* of ZUPANČIČ (1999) where he included relevés of WRABER (1963) from subunits other than *Luzulo sylvaticae-Piceetum sphagnetosum capillifolii* *Carex brizoides*-variant.

<sup>47</sup> I.e. not from the *Vaccinium myrtillus*-variant of WRABER (1963: 115–116, tab. 1). Relevés 8 and 9 might represent a degraded form of *Luzulo sylvaticae-Piceetum calamagrostietosum arundinaceae*.

WILLNER & ZUKRIGL (1999) and WILLNER (2007: 239) proposed the name *Homogyno alpinae-Piceetum Zukrigl 1973* for conservation against the older names *Luzulo sylvaticae-Piceetum Wraber 1963* and *Homogyno alpinae-Piceetum Samek 1961* and explained the reason why the correct date of valid publication of other assumedly synonymous name *Larici-Piceetum* proposed by ELLENBERG & KLÖTZLI (1972) is, in fact, the year 1974.

However, as explained above, the original diagnosis of the association *Luzulo sylvaticae-Piceetum Wraber 1963* represents for the most part anthropogenic degraded *Picea-Fagus* phytocoenoses of the upper montane vegetation zone and the respective relevés should be classified within the class *Carpino-Fagetea*. Therefore, the names *Homogyno alpinae-Piceetum Zukrigl 1973* and *Luzulo sylvaticae-Piceetum Wraber 1963* should not be evaluated as syntaxonomical synonyms, as they belong to two different classes.

The older homonym *Homogyno alpinae-Piceetum Samek 1961 nom. superfl.* (Art. 29c) was already mentioned by ZUKRIGL (1973: 118) and this author also correctly recognized that its original phytocoenological description does not fully correspond with natural supramontane Norway spruce woodlands. As it could be seen from the original diagnosis of the association – and especially of the subassociation *typicum* (SAMEK 1961: 77, Tab. III), the community is mostly based on upper montane secondary *Picea* phytocoenoses of the class *Carpino-Fagetea* (low altitudes, occurrence of *Anemone nemorosa*, *Polygonatum verticillatum*, *Blechnum spicant*). Moreover, SAMEK (1961: 75) (indirectly) published his name as nomen superfluum to *Soldanello montanae-Piceetum* Volk in Br.-Bl. et al. 1939, though Samek used the latter name in the sense of OBERDORFER (1957) (cf. KUČERA 2019b, Suppl. 3, sect. II) instead of intended application of his name as parallel to *Lophozio-Piceetum abietis* Volk in Br.-Bl. et al. 1939 used by TRAUTMANN (1952) which he neglected. One way or another, the original diagnosis of the association *Homogyno alpinae-Piceetum* Samek 1961 and the two theoretically (Art. 18b) possible candidates for a nomenclatural type of the association (from the typical variant) would not allow to evaluate the names *Homogyno alpinae-Piceetum* Samek 1961 and *Homogyno alpinae-Piceetum Zukrigl 1973* as syntaxonomical synonyms.

There also exists an earlier described homonymous name *Homogyno alpinae-Piceetum* Samek et al. 1957 (alternative name, Def. 6) which was not mentioned by WILLNER (2007). However, the subassociation *typicum* of SAMEK et al. (1957) represents for the most part historically degraded forests with anthropogenic absence of *Abies alba* and *Fagus sylvatica*. The subassociation *athyrietasum alpestris* belongs partly to *Athyrio distentifoli-Piceetum abietis* Hartmann ex Hartmann et Jahn 1967 nom. corr. and the habitat-specific subassociation *sphagnetosum acutifolii* is here described as new association *Listero cordatae-Piceetum abietis* (Samek et al. 1957) P. Kučera 2023. Therefore the name *Homogyno alpinae-Piceetum* Samek et al. 1957 should not be considered to be syntaxonomical synonym to *Homogyno alpinae-Piceetum Zukrigl 1973*.

Finally, the most important syntaxonomical circumstance is the typification of the association *Homogyno alpinae-Piceetum Zukrigl 1973* made by WILLNER & ZUKRIGL (1999: 150). The original diagnosis of the association, i.e. synoptic relevé table of ZUKRIGL (1973, tab. II) displays considerable phytocoenotic variation of the respective included subunits. However, the mentioned choice of lectotype relevé (indeed from typical stands of the unit, as proposed by ZUKRIGL [1973]) determined the application of the subassociation *Homogyno alpinae-Piceetum typicum* ( $\equiv$  *Homogyno alpinae-Piceetum myrtilletosum* Zukrigl 1973 [Art. 13b, 14b]) as being

a corresponding name (Def. X) to species-poor association with the correct name *Lophozio-Piceetum abietis* Volk in Br.-Bl. et al. 1939 (= syntax. syn. *Homogyno alpinae-Piceetum* Zukrigl 1973). Therefore, the proposed conservation of the name *Homogyno alpinae-Piceetum* Zukrigl 1973 is redundant and floristically richer natural Norway spruce communities of the Alps, especially phytochorologically different communities including <sup>†</sup>*Rhododendron ferrugineum* etc. should be classified under different names than *Homogyno alpinae-Piceetum* Zukrigl 1973.

## Conclusions

The second version and at the same time fourth part of the syntaxonomical revision of the communities traditionally classified within the class *Vaccinio-Piceetea* Br.-Bl. in Br.-Bl. et al. 1939 from the territory of the Slovak Western Carpathians is presented. It is dedicated to Norway spruce woodlands which are classified within the order *Piceatalia abietis*. The revision is based on careful data selection made in effort to separate the natural supramontane Norway spruce woodlands from the secondary *Picea abies* phytocoenoses, in which evident secondary succession of *Fagus sylvatica* is in progress and which belong to the class *Carpino-Fagetea* Jakucs ex Passarge 1968. The diversity of the Western Carpathian Norway spruce vegetation types found on non-carbonate rocks varying from the most extreme habitats in bouldery scree sites to relatively species-rich acid tall-forb phytocoenoses or moderately waterlogged woodland with partial presence of bog species allows the classification within seven associations arranged in the following scheme:

*Piceatalia abietis* Pawłowski ex Pawłowski et al. 1928 nom. corr.

*Piceion abietis* Pawłowski ex Pawłowski et al. 1928 nom. corr.

*Lophozio-Piceetum abietis* Volk in Br.-Bl. et al. 1939 nom. corr.

*Athyrio distentifolii-Piceetum abietis* Hartmann ex Hartmann et Jahn 1967 nom. corr.

*Solidagini virgaureae-Piceetum abietis* P. Kučera in P. Kučera et al. 2023

*Parido quadrifoliae-Piceetum abietis* P. Kučera in P. Kučera et al. 2023

*Lycopodio annotini-Sorbetum aucupariae* P. Kučera 2023 ass. nov.

*Listero cordatae-Piceetum abietis* (Samek et al. 1957) P. Kučera 2023 ass. nov.

*Sphagno capillifolii-Piceetum abietis* Zukrigl 1973

The most important observation resulting from combined efforts of the thorough field research and subsequent re-evaluation of previously published data and assessments emphasize the need of careful recognition and further field studies of anthropogenic, substitutional *Picea* forests and the elimination of their relevé records from syntaxa of natural Norway spruce woodlands. The example of previously assumed and recently revised data for the Western Carpathians represent an advantageous case study for whole Central Europe. Only such revisions would help to better understand the altitudinal as well as regional distribution of *Vaccinio-Piceetea* communities, their more accurate floristical and phytoconological delimitation and, ultimately, processes associated with the impact of climate change in upper montane and supramontane woodlands. For example, stands of associations *Bazzanio trilobatae-Piceetum* (Schmid et Gaisberg 1936) Br.-Bl. et Sissingh in Br.-Bl. et al. 1939 *Calamagrostio villosae-Piceetum* Schlüter 1966 or *Luzulo sylvaticae-Piceetum* Wraber 1963 as described by their original authors – usually supposed to be elements of Norway spruce zone – do not represent natural Norway spruce woodlands. Ecological and syntaxonomical differentiation between Central European supramontane *Picea abies* (and

*Pinus cembra*) altitudinal vegetation zone and taiga woodland of northern East European to Siberian region with †*Picea obovata* and †*Abies sibirica* is required as well.

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Address of the author:

Peter Kučera  
Belá-Dulice 187  
038 11 Belá-Dulice, Slovakia  
E-mail: peter.kucera@uniba.sk  
ORCID: 0000-0002-8508-616X

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