

Syntaxonomy of relic Swiss stone pine (*Pinus cembra*) forests in the Tatra Mountains

Syntaxonomie der *Pinus-cembra*-Reliktwälder der Tatra

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Abstract

Pinus cembra forests in the Tatra Mountains were studied by MYCZKOWSKI (1970) and WOJTERSKA et al. (2004), and this research led to a description of a separate forest association called *Cembro-Piceetum* Myczkowski 1970 or, according to WOJTERSKA et al. (2004), *Larici-Pinetum cembrae* (Pallmann et Haffter 1933) Ellenberg 1963. However, due to insufficient data, the syntaxonomical status of Swiss stone pine forests remained arguable. Therefore, the aim of this study was to verify the syntaxonomical status of *P. cembra* forests in the Tatra as well as to check the possible occurrence of these forests in the Western Tatra and on calcareous bedrock, which was omitted in earlier studies. We made 108 relevés based on the Braun-Blanquet method throughout the entire range of *P. cembra*. Data collected in the field were numerically analysed based on the modified Marczewski and Steinhaus similarity model. The classification was done for the qualitative and quantitative data using cluster analysis UPGMA. Each relevé was classified fourfold and identified based on the index of phytosociological agreement (IPA). Characteristic and differential species were identified by species percentage frequency, fidelity, cover ratio and dominance ratio. We determined two main syntaxonomical units of relic Swiss stone pine forests, *Vaccinio-Pinetum cembrae* (Pallmann & Haffter 1933) Oberdorfer 1962 and, on calcareous ground, *Swertio perennis-Pinetum cembrae* ass. nov. The *Vaccinio-Pinetum cembrae* was divided into two subassociations and three variants, while the *Swertio perennis-Pinetum cembrae* occurred in two variants. To establish their syntaxonomical status, data collected in the field were compared with relevés collected from the Tatra upper montane *Picea abies* forests, Tatra *Pinus mugo* shrubs, and Alpine *P. cembra* forests. Results of similarity analyses showed that relic *P. cembra* forests in the Tatra growing on granite bedrock are a distinct plant association, different from the *Plagiothecio-Piceetum*, and should be treated as one Swiss stone pine forest association *Vaccinio-Pinetum cembrae*, common to the Alps and to the Tatra. Furthermore, this study documented the occurrence of *P. cembra* forests in the Western Tatra.

Keywords: *Vaccinio-Pinetum cembrae*, *Swertio perennis-Pinetum cembrae*, phytosociology, Tatra Mountains, Central European upper montane forests, numerical classification

Erweiterte deutsche Zusammenfassung am Ende des Artikels

1. Introduction

Relic Swiss stone pine (*Pinus cembra*) forests were among the least studied plant associations in the Western Carpathians. Due to an insufficient number of phytosociological surveys in these forests, their syntaxonomical status was arguable (MATUSZKIEWICZ 2008). On the other hand, these forests play an important role in the regional conservation of biodiversity. Their two main components, *P. cembra* and European larch (*Larix decidua* subsp. *decidua*), are extremely rare in the Western Carpathians, and Swiss stone pine occurs as a native tree only in the Tatra (HOLEKSA & SZWAGRZYK 2004).

There is historical evidence that both species had been heavily harvested in the Tatra due to their precious wood (JAMNICKÝ 1964, PARYSKI 1971, MADEYSKI 1974). Human impact meant that *P. cembra* forests survived only in the least accessible places along the timberline. These woods in some parts of the Tatra can be regarded as virgin forests. According to some authors these refugia resemble the first type of forest that occurred in the Tatra at the transition between the Ice Age and Holocene ca. 12,000 years BP (SZAFER 1966, BEDNARZ 1969, OBIDOWICZ et al. 2004).

The first scientific surveys of *P. cembra* forests were made in the early 20th century. SOKOŁOWSKI (1928) distinguished in some parts of the Tatra a separate belt of *P. cembra* above the spruce forests. Nonetheless, at the time of the first phytosociological studies, *P. cembra* forests were considered rare and specific subtypes of the widespread spruce forest *Piceetum excelsae (tatricum)* (PAWŁOWSKI et al. 1928). Nowadays it is called *Plagiothecio-Piceetum* (Szafer, Pawłowski et Kulczyński 1923) Braun-Blanquet, Vliieger et Sissingh 1939 em. Matuszkiewicz 1977 (MATUSZKIEWICZ 1977, MATUSZKIEWICZ 2008).

Further studies on Swiss stone pine forests were carried out by MYCZKOWSKI (1969). He proposed one association for all Eurasian *P. cembra* forests, divided into several subassociations depending mostly on geographical criteria. Finally MYCZKOWSKI (1970) described an association *Cembro-Piceetum* Ellenberg 1968 – relic Swiss stone pine forests of the Tatra Mountains, within the alliance *Piceion excelsae*. Presently, synonyms of this association are *Cembro-Piceetum* Myczkowski 1970 or *Pino cembrae-Piceetum* Myczkowski & Lesiński 1974. MYCZKOWSKI (1970) stressed greater plant diversity within the *P. cembra* forests in comparison to upper montane spruce forests and similarities in the *Cembro-Piceetum* and the *Larici-Pinetum cembrae* Ellenberg 1963 in the Alps (MYCZKOWSKI 1969, 1970, 1971, MYCZKOWSKI & BEDNARZ 1974, MYCZKOWSKI & LESIŃSKI 1974).

Since then, only one study conducted on *P. cembra* forests in the Western Carpathians has been published (WOJTERSKA et al. 2004). The syntaxonomical status of the *Cembro-Piceetum* was challenged in a recent synthesis of Polish plant communities by MATUSZKIEWICZ (2008). According to him any aggregation of *P. cembra* should be considered as a local form of the upper montane spruce forest *Plagiothecio-Piceetum*, limited to the High Tatra and to granite bedrock. However, he suggested further research concerning this issue (MATUSZKIEWICZ 2008). The syntaxonomy of *P. cembra* forests gets even more complex, when we consider the Slovakian part of the Tatra Mountains. A lack of a unified study for the entire Tatra, as well as different approaches in describing vegetation in Slovakia led to the emergence of different classifications of *P. cembra* forests, mostly based on forest typology (DRAŽIL 2002).

A benchmark for relic *P. cembra* forests in the Tatra is a broad belt of subalpine Swiss stone pine-larch forests (*Vaccinio-Pinetum cembrae* (Pallman & Haffter 1933) Oberdorfer 1962, syn. *Larici-Pinetum cembrae* Ellenberg 1963) in the Alps (ELLENBERG 1963, 1978, WALLNÖFER 1993, WILLNER & GRABHERR 2007). Alpine *Pinus cembra-Larix* forests were

described for the first time in the works of SCHRÖTER (1926) and PALLMANN & HAFFTER (1933). However, ELLENBERG (1963) was the first scientist to introduce them permanently to phytosociological nomenclature. It is worth stressing that *P. cembra* forests according to Ellenberg's idea belong to a separate suballiance: *Rhododendro-Vaccinienion* Braun-Blanquet 1926, which emphasizes the difference between them and the group of upper montane spruce forests *Vaccinio-Piceenion*. Likewise, WILLNER & GRABHERR (2007) in their synthesis of Austrian plant communities classified *P. cembra* forests into a group of subalpine scrub vegetation (*Pinion mugo* Pawłowski 1928 within the order *Junipero-Pinetalia mugo* Boşcaiu 1971), separate from typical spruce forests. Furthermore, ELLENBERG (1978) described Swiss stone pine forests from the Tatra together with their Alpine counterparts, highlighting their common features.

The incorporation of *P. cembra* forests of the Tatra Mountains as Natura 2000 habitat type into Annex I of the Habitats Directive (code: 9420) caused an urgent need for deeper understanding of these precious forests (HOLEKSA & SZWAGRZYK 2004, MRÓZ et al. 2012). Therefore the aim of this work was (1) to settle the syntaxonomical status of *P. cembra* forests in the Tatra on the basis of a large number of relevés collected over the entire mountain range and (2) to investigate the occurrence of these forests in the Western Tatra, as well as on calcareous bedrock, which has been unregarded during earlier studies on *P. cembra* forests conducted in the Tatra.

2. Study area

The Tatra are the highest mountains in the entire Carpathians (highest peak: Gerlach 2655 m a.s.l.) divided between Poland and Slovakia. The total area of the Tatra is only 785 km². Based on geomorphological criteria, the Tatra Mountains are divided into three separate parts: Western Tatra, High Tatra and Belianske Tatra (RADWAŃSKA-PARYSKA & PARYSKI 2004). They are an island of alpine-type landscape in the Western Carpathians, with well-developed mountain vegetation belts (up to the sub-nival zone) (MIREK 1996). High altitude, geographic isolation and diverse bedrock caused the survival of unique fauna and flora. The Tatra are home to many endemic, relict and rare species, habitats, remains of virgin forests and three big European predators – brown bear, wolf and lynx. They are a biodiversity hotspot with ca. 1,300 species of vascular plants and 6,000 species of animals (MIREK 1996, MIREK & PIĘKOŚ-MIRKOWA 2003, SKRZYDŁOWSKI 2013, MRÁZ & RONIKIER 2016, MRÁZ et al. 2016). Due to these attributes they are a National Park (IUCN PA management category II), an International MAB UNESCO Biosphere Reserve and belong to the Natura 2000 network (SPA & SAC) (SKRZYDŁOWSKI 2013).

Relic *P. cembra* forests occur in the Tatra in the upper montane belt, close to the timberline, ca. 1300–1600 m a.s.l. (MYCZKOWSKI & BEDNARZ 1974). The geological formations vary but consist mostly of granite, limestone, dolomite and quartz sandstone. The soils that developed on such bedrocks are podzols, rendzina and rankers (PASSENDORFER 1996, PIOTROWSKA et al. 2015, SKIBA et al. 2015). *Pinus cembra* forests grow in the Tatra in the zone of cool climate with a mean annual temperature of +3 °C and mean annual sum of precipitation of 1400 mm (HESS 1996, USTRNUL et al. 2015, ŹMUDZKA et al. 2015). Snow cover lasts for ca 150 days/year (USTRNUL et al. 2015).

3. Methods

3.1 Data collection

The concept of the field work was to collect relevés in every major valley within the entire distribution range of *P. cembra* in the Tatra (Fig. 1). The research area represented the entire diversity of bed-rock (quartz sandstone, granite, limestone, dolomite) on which Swiss stone pine occurs in the Western Carpathians. Localization of relevés was based on certain criteria, such as homogeneity and representativeness of phytocoenoses (KENT & COKER 1992, DZWONKO 2008), as well as a share of more than 20% of *P. cembra* in the forest stand. In valleys where *P. cembra* occurred sparsely, the third criterion was disregarded and relevés were made wherever Swiss stone pines grew. Furthermore, in some valleys relevés were taken in adjacent patches of spruce forests. Altogether, 108 relevés were made according to the Braun-Blanquet method (KENT & COKER 1992, DZWONKO 2008). The species coverage was determined for each layer of the forest (A – stand layer, including each sublayer of the stand: A1, A2; B – shrub layer, C – herb layer, D – moss layer). The majority of the relevés had a size of 250 m²; however, some of them were smaller (down to 100 m²) due to topographic constraints (cliff forests). The locations of the relevés were recorded as geographical coordinates and altitude at the centre of the plot, exposure with azimuth [°] and slope inclination [°]. The diameter at breast height (dbh) [cm] and height [m] of selected trees were also measured; tree age was estimated visually and the physiography of the terrain was described. The relevés are stored in the Forest Database of Southern Poland (PIELECH et al. 2018).

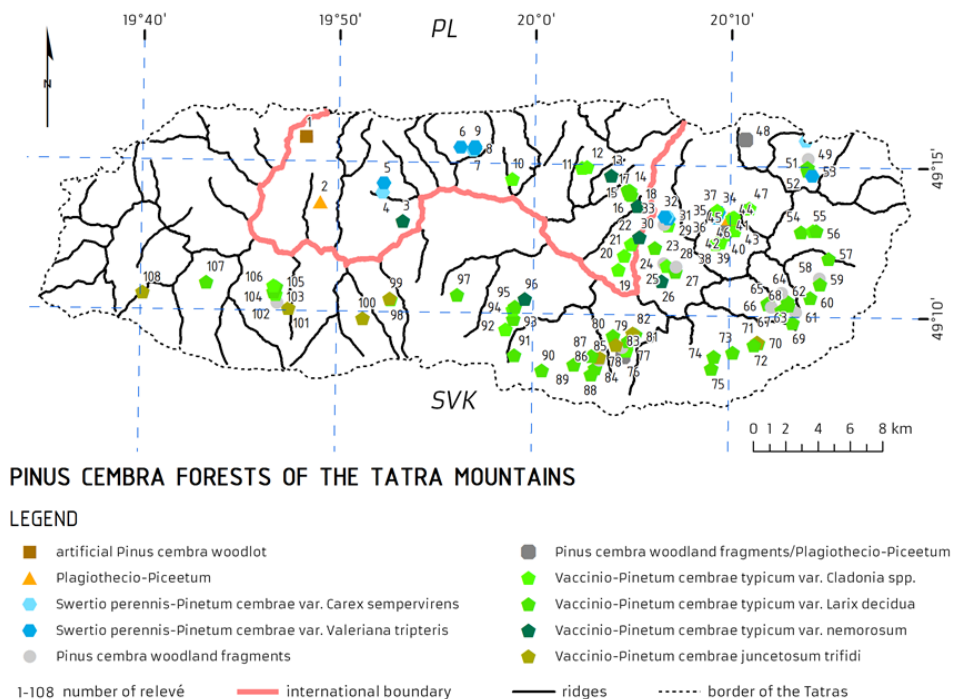


Fig. 1. Location of relevés representing the relic Swiss stone pine forests and adjacent forests in the Tatra Mountains (source: GIS of the Tatra National Park).

Abb. 1. Lage der Aufnahmeflächen der Zirbel-Kiefern- und angrenzender Wälder in der Tatra.

Furthermore, to verify the syntaxonomical status of relic Swiss stone pine forests in the Tatra, data collected in the field were compared with 21 relevés of upper montane spruce forests (*Plagiothecio-Piceetum*) and calcicolous upper montane spruce forests (*Polysticho-Piceetum* [Szafer, Pawłowski et Kulczyński 1923] Matuszkiewicz [1967] 1977), from the Tatra (data taken from: MATUSZKIEWICZ et al. 2007), as well as with 46 relevés of subalpine *Pinus mugo* krummholz from the Tatra: *Vaccinio myrtilli-Pinetum mugo* (Pawłowski, Sokołowski et Wallisch 1926) Hadač 1956, *Athyrio distentifolii-Pinetum mugo* (Sillinger 1933) Hadač 1956 (data taken from: SZCZYGIELSKI 2001). These are the communities directly bordering the Swiss stone pine forests and the closest ones in terms of syntaxonomy. In addition to that, to investigate the syntaxonomical relation between the Tatra and Alpine *P. cembra* forests, the analysed data set was extended by 98 relevés from the Austrian Alps, representing the association *Vaccinio-Pinetum cembrae*, received from the Austrian Vegetation Database (WILLNER et al. 2012).

3.2 Data analysis

The set of 108 relevés was analysed with numerical methods based on the agglomerative cluster analysis. For the classification of relevés we used the unweighted pair group method using arithmetic averages (UPGMA) (SNEATH & SOKAL 1973, DZWONKO 2008). Each relevé was UPGMA classified fourfold, using different transformation of the initial data matrix (Table 1) (BODZIARCZYK et al. 2016).

Similarity matrices were computed using the modified Marczewski and Steinhaus model, which is a generalized qualitative Jaccard formula (RÓŻAŃSKI 1988):

$$CS_{R1Q} = \frac{4 \sum_{i=1}^n \min(x_{ik}, x_{il}) \sum_{i=1}^n x_{ik} \sum_{i=1}^n x_{il}}{[\sum_{i=1}^n (x_{ik} + x_{il}) - \sum_{i=1}^n \min(x_{ik}, x_{il})][\sum_{i=1}^n (x_{ik} + x_{il})]^2}$$

where

CS_{R1Q} - similarity according to modified formula of Marczewski and Steinhaus, between relevés "k" and "l";

x_{ik} - quantitative level of species "i" in relevé "k";

x_{il} - quantitative level of species "i" in relevé "l";

n - overall number of species in data set.

Afterwards, each of the four matrices was grouped based on UPGMA (SNEATH & SOKAL 1973, DZWONKO 2008). Results were visualized in four dendrograms. Based on each dendrogram, we constructed four preliminary phytosociological tables. According to this method, each relevé was identified into clusters fourfold. Based on that, we calculated the index of phytosociological agreement (IPA), which was used later in the final syntaxonomical identification (BODZIARCZYK et al. 2016). In this method, the most homologous relevés (IPA = 1.0 – unequivocal relevés) were those that, according to each of the four variants of the cluster analysis, showed the same identity. The lowest acceptable level of IPA was 0.5 (fuzzy relevés) (Table 2) (BODZIARCZYK et al. 2016).

According to the dendrograms and results of the IPA we conducted on the syntaxonomical classification of 108 relevés we prepared the final phytosociological tables of the determined syntaxa.

Characteristic and differential species were determined by species percentage frequency (N%), fidelity (F) and cover ratio (CR) (PAWŁOWSKI 1977, DIERSCHKE 1994). In addition to that, to assign diagnostic species we used the dominance ratio (DR) as proposed by RÓŻAŃSKI (1991):

$$\forall CR \geq 1; DR = N\% \times \frac{\log CR}{\log 8750};$$

$$\forall CR < 1; DR \stackrel{\text{def}}{=} 0;$$

DR – dominance ratio of species in plant association;

CR – mean cover ratio of species in plant association according to Braun-Blanquet scale;

$N\%$ – percentage frequency of species in plant association.

\forall – if.

Table 1. Variants of transformation of data set into computational matrix.**Tabelle 1.** Transformationsvarianten bei der Matrix-Erstellung.

Variants of data transformation	Braun-Blanquet's cover-abundance scale							
	R	+	1	2	3	4	5	Species absence
A binary – qualitative scale; all species in all layers	1	1	1	1	1	1	1	0
B “neutral” – quantitative scale; all species in all layers	1	1	2	3	5	7	9	0
C “neutral” – quantitative scale; species only from the shrubs and forest floor vegetation (layers B, C, D)	1	1	2	3	5	7	9	0
D average percentage of cover-age; all species in all layers	0.1	0.1	5	17.5	37.5	62.5	87.5	0

Table 2. The criteria of establishing the Index of phytosociological agreement (IPA) (BODZIARCZYK et al. 2016).**Tabelle 2.** Kriterien für die Erstellung des Index der pflanzensoziologischen Übereinstimmung (IPA) (BODZIARCZYK et al. 2016).

IPA		Combinations of the results of various classification of the relevés based on the four variants of transformation of initial data matrix (see Table 1)
Numerical value	Name	
1,00	unequivocal	in all variants relevé was classified alike
0.75	meaningful	in three of four variants relevé was classified alike
0.50	fuzzy	in two of four variants relevé was classified alike
0,00	lack of agreement	in none variant relevé was classified alike

The nomenclature of the vascular plants followed MIREK et al. (2002), of bryophytes OCHYRA et al. (2003) and of lichens FAŁTYNOWICZ & KOSSOWSKA (2016). The names of higher-rank syntaxa (class, order, alliance) followed MUCINA et al. (2016), whereas the names of plant associations from the Carpathians were given after MATUSZKIEWICZ (2008), and from the Alps followed WILLNER & GRABHERR (2007). The nomenclature of newly described syntaxonomical units followed the International Code of Phytosociological Nomenclature (WEBER et al. 2000). The proposed classification of *P. cembra* forests followed the standardized hierarchical syntaxonomic system of European plant communities (MUCINA et al. 2016).

To verify the syntaxonomical status of the Swiss stone pine forests of the Tatra, the results of our classification were compared to the closest plant communities from the Tatra and from the Alps. In the case of the *Vaccinio-Pinetum cembrae*, for the analysis we took only relevés representing the typical subassociation (*-typicum*) – 69 relevés from the Tatra and 98 from the Alps (Fig. 3, Table 3). The following parameters were analysed: percentage frequency, cover ratio and dominance ratio. The calculation procedure was similar to that used in the previous analysis, including similarity matrices based on modified Marczewski and Steinhaus model and UPGMA.

All calculations were done using original software developed at the Department of Forest Biodiversity at the University of Agriculture in Krakow (Poland).

4. Results and Discussion

4.1 Classification of relic *Pinus cembra* forests in the Tatra

On the basis of the multivariate numerical analysis of 108 relevés we determined two units in the rank of association and a group of relevés with unclear syntaxonomic status: (1) relic *P. cembra* forest *Vaccinio-Pinetum cembrae*, (2) relic calcicolous *P. cembra* forests of the Tatra Mountains *Swertio perennis-Pinetum cembrae* ass. nov., and (3) *P. cembra* woodland fragments – a group of relevés with an imprecise syntaxonomical status, including relevés classified as *Plagiothecio-Piceetum* (Supplements S1–S3).

4.1.1 *Vaccinio-Pinetum cembrae* (Pallmann & Haffter 1933) Oberdorfer 1962 (syn. *Larici-Pinetum cembrae* Ellenberg 1963, *Pino cembrae-Piceetum* Myczkowski & Lesiński 1974) – relic *Pinus cembra* forest (Supplement S2)

ChAss.: *P. cembra*, *Gentiana punctata*, *Sphagnum quinquefarium*, *Cladonia macroceras*

DAss.: *Larix decidua*, *Sorbus aucuparia* var. *glabrata* (A), *Salix silesiaca*, *Betula pubescens* subsp. *carpatica*, *Vaccinium vitis-idaea*, *Veratrum lobelianum*, *Rhytidiadelphus triquetrus*, *Cetraria islandica*

This association develops on silicate rocks of the Tatra Mountains, in the upper montane belt, close to the timberline (1256–1690 m a.s.l., average: 1486 m a.s.l.). Relic *P. cembra* forests have mostly a character of cliff forests growing on steep and rocky slopes (average inclination: 31°). A stand has usually two layers (A1, A2) and consists of *P. cembra* (N%: 94.8%, F: V, CR: 3656, DR: 85.7 – values of parameters of tree species represent layer A1; for layer A2, see Supplement S2–S3), *Picea abies* (N%: 92.2%, F: V, CR: 2498, DR: 79.5), *Larix decidua* – predominantly on the southern slopes of the Tatra (N%: 42.9%, F: III, CR: 296, DR: 26.9), with admixture of *Sorbus aucuparia* var. *glabrata*, *Salix silesiaca* and *Betula pubescens* subsp. *carpatica*. Another characteristic feature of this association is a well-developed shrub layer with *Pinus mugo* (N%: 97.4%, F: V, CR: 2348, DR: 83.3) and admixture of *Juniperus communis* subsp. *alpina*, as well as all the tree species mentioned above. The ground layer (C) is dominated by two *Vaccinium* species: *V. myrtillus* (N%: 98.7%, F: V, CR: 5500, DR: 93.7), *V. vitis-idaea* (N%: 98.7%, F: V, CR: 2286, DR: 84.1) and other plants typical for the alliance *Piceion excelsae*. A relatively low cover of the tree layer (70%) enables the appearance of typical high alpine meadow species, such as *Gentiana punctata* (N%: 27.3%, F: II, CR: 53.1, DR: 11.9) and *Veratrum lobelianum* (N%: 32.5%, F: II, CR: 7.73, DR: 7.31). The moss layer (D) is well developed with average cover of 64%. The characteristic feature of this layer is the abundance of *Sphagnum quinquefarium* (N%: 58.4%, F: III, CR: 1802, DR: 48.3). Other common species are *Dicranum scoparium*, *Pleurozium schreberi*, *Hylocomium splendens*, *Polytrichastrum formosum* and *Rhytidiadelphus triquetrus*. Furthermore, it is worth to emphasize the frequent presence of lichens represented mostly by *Cladonia* spp. and *Cetraria islandica*.

Based on our analyses the *Vaccinio-Pinetum cembrae* in the Tatra has been divided into two subassociations and three variants:

1) *Vaccinio-Pinetum cembrae* subass. *typicum* var. *Larix decidua*

This variant occurs predominantly on the eastern and southern slopes. It is characterized by a larger share of *L. decidua* (N%: 60.5%, F: IV, CR: 474, DR: 41.1), as well as of *Betula pubescens* subsp. *carpatica*, *Juniperus communis* subsp. *alpina* and *Calamagrostis villosa*.

2) *Vaccinio-Pinetum cembrae* subass. *typicum* var. *Cladonia* spp.

This variant occurs mostly on the western and northern slopes. In comparison to the previous variant, it is characterized by a relatively low share of *L. decidua*, as well as a higher frequency of lichens in the D layer, including *Cetraria islandica* and *Cladonia* spp. (especially *Cladonia macroceras*). In the herb layer we recorded a frequent occurrence of *Gentiana punctata* and *Lycopodium annotinum*. The moss layer is dominated by *Sphagnum quinquefarium* (N%: 88%, F: V, CR: 3710, DR: 79.7). Furthermore, it is the only variant with a relatively high frequency of *Mytilus taylori*.

3) *Vaccinio-Pinetum cembrae* subass. *typicum* var. *Gymnocarpium dryopteris*

This variant develops on very steep (average inclination: 48°) and rocky slopes. It is characterized by dense stands (average cover: 92%) and relatively low cover in the shrub layer (13%). The herb layer has a low number of species. The moss layer is dominated by *Sphagnum quinquefarium*.

4) *Vaccinio-Pinetum cembrae juncetosum trifidi* subass. nov. hoc loco

Typus: Supplement S2, rel. 82 – holotypus hoc loco (Fig. 2a)

This subassociation encompasses the highest woodland areas in the Tatra (average elevation: 1564 m a.s.l.; max: 1690 m a.s.l.). A low cover in the tree layer (63%) enables the occurrence of Alpine plant species representing the class *Juncetea trifidi* Hadač in Klika et Hadač 1944, such as *Festuca airoides*, *Juncus trifidus* and *Oreochloa disticha*, and of species of subalpine scrub and tundra (classes *Roso pendulinae-Pinetea mugo* Theurillat in Theurillat et al. 1995 and *Loiseleurio procumbentis-Vaccinietae* Eggler ex Schubert 1960), such as *Pinus mugo*, *Juniperus communis* subsp. *alpina*, *Empetrum hermaphroditum*, and of the class *Mulgedio-Aconitetea* Hadač et Klika in Klika et Hadač 1944, including *Ranunculus platanifolius*, *Senecio nemorensis*, *Solidago alpestris*, and *Adenostyles alliariae*. Furthermore, species representing *Piceetalia excelsae* and *Piceion excelsae* are less numerous and abundant in comparison to the other variants. A scattered canopy together with rocky ground favours the growth of other light-demanding species, such as *Calluna vulgaris*, *Campanula polymorpha*, *Sempervivum montanum* and several species of lichens, including *Cetraria islandica* and *Cladonia* spp. (mostly *C. macroceras*, *C. rangiferina*).

**4.1.2 *Swertio perennis-Pinetum cembrae* ass. nov. hoc loco –
calicolous relic Swiss stone pine forest of the Tatra Mountains (Supplement S3).**

Typus: Supplement S3, rel. 33 – holotypus hoc loco (Fig. 2b)

ChAss.: *Pinus cembra*, *Swertia perennis*

DAss.: *Carex sempervirens*, *Valeriana tripteris*, *Saxifraga paniculata*, *Scabiosa lucida*, *Melampyrum herbichii*, *Campanula polymorpha*, *Sphagnum quinquefarium*, *Tortella tortuosa*

This association occurs on steep (average inclination: 40°) limestone and dolomite rocks in the upper montane belt (1315 (1039)–1562 m a.s.l.), close to the timberline. A stand has usually two layers (A1, A2) and consists of *P. cembra* (N%: 100%, F: V, CR: 2912.3, DR: 87.9), *Picea abies* (N%: 85.7%, F: V, CR: 1965.7, DR: 71.6) with an admixture of *Sorbus aucuparia* var. *glabrata*. A well-developed shrub layer consists of *Pinus mugo* (N%: 57.1%, F: III, CR: 965.1, DR: 43.3), *Sorbus aucuparia* var. *glabrata* (N%: 71.4%, F: IV, CR: 165, DR: 40.2), *Salix silesiaca* (N%: 71.4%, F: IV, CR: 147.2, DR: 39.3) and *Lonicera nigra* (N%: 50%, F: III, CR: 3.7, DR: 7.2).

As in the silicate relic *P. cembra* forests, the herb layer is dominated by *Vaccinium myrtillus* (N%: 85.7%, F: V, CR: 3017.9, DR: 75.7) and *V. vitis-idaea* (N%: 92.9%, F: V, CR: 1517.9, DR: 74.9). The ground layer is composed on the one hand by species typical for the class *Vaccinio-Piceetea* and on the other by species confined to rich calcareous soils, such as: *Carex sempervirens*, *Saxifraga paniculata* and *Scabiosa lucida*. It is worth stressing the constant presence of *Swertia perennis*, which is the characteristic and name giving species for this syntaxon. The moss layer (D) is well developed with an average cover of 56%. The most abundant species are *Hylocomium splendens*, *Polytrichastrum formosum*, *Pleurozium schreberi*, *Tortella tortuosa*, *Rhytidiadelphus triquetrus* and *Hypnum cupressiforme*. Furthermore, it is worth emphasizing, despite the calcareous soils, the relatively high cover of the typically acidophilous moss *Sphagnum quinquefarium* (N%: 28.6%, F: II, CR: 660.7, DR: 20.4). The association *Swertia perennis-Pinetum cembrae* can be divided into two variants:

1) *Swertia perennis-Pinetum cembrae* var. *Valeriana tripteris*

This variant is characterized by a constant presence of *Valeriana tripteris* (N%: 100%, F: V, CR: 355.1, DR: 64.7). In the ground layer, despite the dominance of *Vaccinio-Piceetea* species, there are also mesophilous species of the lower montane belt, mostly representing the class *Carpino-Fagetea sylvaticae* Jakucs ex Passarge 1968, such as *Prenanthes purpurea*, *Astrantia major* and *Phyteuma spicatum*. Moist limestone and dolomite cliffs enable the growth of various pteridophytes: *Asplenium viride*, *Cystopteris fragilis* and *Polypodium vulgare*. The relatively scattered tree canopy (average coverage: 77%) favours the occurrence of plants representing *Adenostyletalia alliariae* Braun-Blanquet 1930, like *Polygonatum verticillatum*, *Senecio nemorensis*, *Veratrum lobelianum*, *Solidago alpestris* and *Adenostyles alliariae*.

2) *Swertia perennis-Pinetum cembrae* var. *Carex sempervirens*

This variant represents open *P. cembra* woodlands (average A layer coverage: 35%) on exposed, steep (average inclination: 54°) limestone and dolomite rocks (Fig. 2c). Such conditions foster the growth of numerous species representing rich calcareous alpine swards of *Elyno-Seslerietea* Braun-Blanquet 1948. On the other hand, we recorded the unexpected occurrence of typically acidophilous species, such as *Vaccinium gaultherioides* and *Empetrum hermaphroditum*. Furthermore, this type of relic *P. cembra* forest shows the lowest share of *Vaccinio-Piceetea* plants among all *P. cembra* communities in the Tatra.

4.1.3 *Pinus cembra* woodland fragments

This group consists of 17 relevés with uncertain syntaxonomical status. In the dendrograms (Supplement S1) we can see them as being separated both from the typical *Vaccinio-Pinetum cembrae* (centre of dendrograms) and the *Swertia perennis-Pinetum cembrae*. Some of the relevés representing *P. cembra* woodland fragments are transitional between relic *P. cembra* forests and upper montane spruce forests, whereas others seem to represent the typical *Plagiothecio-Piceetum*.

4.2 Syntaxonomical status of relic *Pinus cembra* forests in the Tatra

The results of the similarity analysis of species percentage frequency, cover ratio and dominance ratio between the previously mentioned plant communities supported the hypothesis that relic *P. cembra* forests in the Tatra are separate plant associations, distinct from the

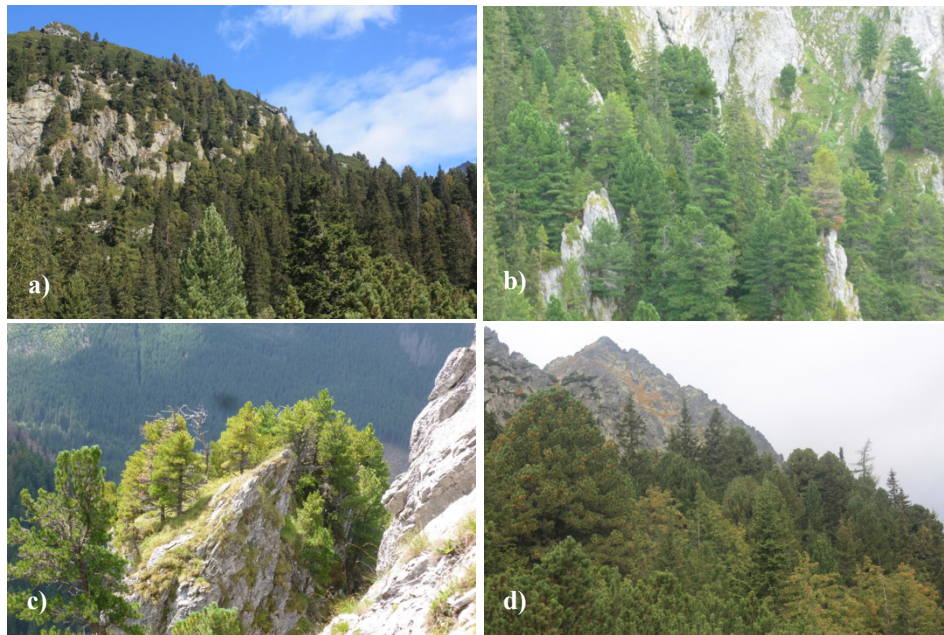


Fig. 2. **a)** Open *Vaccinio-Pinetum cembrae juncetosum trifidi* subass. nov. forest near location of relevé 82 (holotypus hoc loco) on the steep cliffs in Mięguszowiecka Valley (Tatra Mountains). **b)** Calcicolous relic Swiss stone pine forest *Swertio perennis-Pinetum cembrae* ass. nov. near location of relevé 33 (holotypus hoc loco) in Biała Woda Valley (Tatra Mountains). **c)** *Swertio perennis-Pinetum cembrae* var. *Carex sempervirens* woodlands on exposed and steep limestone and dolomite rocks in Biała Woda Valley (Tatra Mountains). **d)** Characteristic physiognomy of *Vaccinio-Pinetum cembrae* forests with multi-layered stand consisting of *P. cembra*, *L. decidua*, *P. abies*, *S. aucuparia* var. *glabrata* and well-developed shrub layer with *P. mugo* (Tatra Mountains) (Photos: A. Zięba, August–September 2013).

Abb. 2. **a)** Offenwald des *Vaccinio-Pinetum cembrae juncetosum trifidi* subass. nov. nahe der Holotypus-Aufnahmefläche 82 auf schroffen Felswänden im Mięguszowiecka-Tal (Tatra). **b)** Zirbel-Kiefern-Reliktwald über Kalk (*Swertio perennis-Pinetum cembrae* ass. nov.) nahe der Holotypus-Aufnahmefläche 33 im Tal Biała Woda (Tatra). **c)** Wald des *Swertio perennis-Pinetum cembrae* var. *Carex sempervirens* auf exponierten und steilen Kalk- und Dolomittfelsen im Tal Biała Woda (Tatra). **d)** Charakteristisches Erscheinungsbild von mehrschichtigen Beständen des *Vaccinio-Pinetum cembrae* in der Tatra aus *Pinus cembra*, *Larix decidua*, *Picea abies*, *Sorbus aucuparia* var. *glabrata* und einer gut ausgebildeten Strauchschicht mit *Pinus mugo*.

Plagiothecio-Piceetum. Furthermore, the *P. cembra* forests in the Tatra are more closely related to their counterparts in the Alps than to the bordering upper montane spruce forests (Fig. 3). This is in contrast to MATUSZKIEWICZ (2008) and supports the concept of a single *P. cembra* forest association, common to the Alps and the Tatra and divided into geographical variants (MYCZKOWSKI 1969, ELLENBERG 1978). Diagnostic species are chiefly the same (WILLNER & GRABHERR 2007), differing at most by strictly regional species, such as *Rhododendron ferrugineum* in the Alps and *Salix silesiaca* in the Tatra (Table 3).

Pinus cembra forests seem to be closer related to upper montane spruce forests of the *Vaccinio-Piceenion* than to subalpine *P. mugo* krummholz (*Rhododendro-Vaccinienion* according to ELLENBERG 1978 or *Pinion mugo* according to WILLNER & GRABHERR 2007) (Fig. 3). Therefore, we suggest the following classification of the relic *P. cembra* forests in the Tatra Mountains:

- Cl.: *Vaccinio-Piceetea* Br.-Bl. in Br.-Bl. et al. 1939
 O.: *Piceetalia excelsae* Pawł. et al. 1928
 All.: *Piceion excelsae* Pawł. et al. 1928
 Suball.: *Vaccinio-Piceenion* Oberd. 1957
 Ass.: *Vaccinio-Pinetum cembrae* (Pallmann & Haffter 1933) Oberd. 1962
 Alpine and relic silicate Tatra Swiss stone pine forest (77 relevés)
 Subass. *V.-P.c. typicum* (69 relevés)
 Var. *Larix decidua* (38 relevés)
 Var. *Cladonia* spp. (25 relevés)
 Var. *Gymnocarpium dryopteris* (6 relevés)
 Subass. *V.-P.c. juncetosum trifidi* subass. nov. hoc loco (8 relevés)
 Ass.: *Swertio perennis-Pinetum cembrae* ass. nov. hoc loco
 Relic calcicolous Swiss stone pine forest of the Tatra Mountains
 (14 relevés)
 Var. *Valeriana tripteris* (10 relevés)
 Var. *Carex sempervirens* (4 relevés)

The problem regarding the classification of *P. cembra* forests into the suballiance *Vaccinio-Piceenion* or into subalpine krummholz vegetation is directly related to the occurrence along the timberline, transitional between forest and subalpine shrublands. Parts of the *Vaccinio-Pinetum cembrae* growing at the lower elevation are more similar to *Vaccinio-Piceenion* forests, whereas those growing at their upper limits resemble *Pinion mugo* krummholz with scattered groups of trees. This seems to be visible also in the results of our classification. The majority of the Tatra *Vaccinio-Pinetum cembrae typicum* forests growing at the mean altitude 1476 m a.s.l. have a character of double-layered forests with mean cover of the tree layer about 70%. This is ca. 70 m below the timberline (1550 m a.s.l.) in the Tatra, and at such an elevation spruce forests also grow well. On the other hand, the highest *P. cembra* woodlands in the Tatra of *Vaccinio-Pinetum cembrae juncetosum trifidi* grow at a mean altitude of 1564 m. a.s.l., which is above the theoretical timberline and zone of spruce forests in this mountain range. *Vaccinio-Pinetum cembrae juncetosum trifidi* has the character of open stands, or even groups of trees in the subalpine vegetation mostly representing *Pinion mugo* (Fig. 2a).

Therefore, it is hard to unequivocally classify these forests to one of the mentioned above syntaxa. However, based on the results of the similarity analysis we propose to include them into *Vaccinio-Piceenion*. The fact of the occurrence of species representing *Pinion mugo* emphasizes their transitional character along the timberline and distinctiveness from the typical upper montane spruce forests. Differences between ELLENBERG (1978) and WILLNER & GRABHERR (2007) and our results might be due to quite often scattered *P. cembra* stands in the Alps in comparison to the Tatra. This might be partly caused by silvopasture in the Alps, which supports open stands, whereas in the Tatra pastoralism has been abandoned since 1960/1970s (RADWAŃSKA-PARYSKA & PARYSKI 2004). Furthermore, *P. cembra* forests survived in the Tatra chiefly in the most inaccessible places, without any impact from cattle or sheep grazing.

The results of our study seem to confirm the recent hierarchical floristic classification system of the European vascular plant communities (MUCINA et al. 2016) where *P. cembra* forests were classified into the *Piceion excelsae*, defined as an alliance of the European boreo-montane spruce forests and subalpine open pine woods on nutrient poor podzolic

Table 3. Synoptical table of the upper montane spruce forests of the Tatra Mountains (*Plagiothecio-Piceetum* – 12 relevés), the calcicolous upper montane spruce forests from the Tatra Mountains (*Polysticho-Piceetum* – 9 relevés), relic calcicolous Swiss stone pine forests of the Tatra Mountains (*Swertio perennis-Pinetum cembrae* – 14 relevés), relic *Pinus cembra* forests from the Tatra (*Vaccinio-Pinetum cembrae typicum* – 69 relevés) and from the Alps (*Vaccinio-Pinetum cembrae typicum* – 98 relevés). Species which do not exceed the constancy threshold – II, and species which had the II constancy class but do not represent any of the important syntaxonomical groups for diagnosis of the upper montane spruce and Swiss stone pine forests were omitted in the table. On the other hand we included in the synoptic table species with constancy class I, which were important for distinguishing Swiss stone pine communities from the other. Symbols: C: constancy (the percentage of relevés in which the certain taxon is present (PAWŁOWSKI 1977): I: 0–20%, II: 21–40%, III: 41–60%, IV: 61–80%, V: 81–100%), CR: cover ratio (representing the mean cover of given species in the relevés in the table multiplied by 100 (DIERSCHKE 1994).

Tabelle 3. Synoptische Tabelle der hochmontanen Fichtenwälder der Tatra (*Plagiothecio-Piceetum* – 12 Vegetationsaufnahmen), der hochmontanen Kalk-Fichtenwälder der Tatra (*Polysticho-Piceetum* – 9 Aufnahmen), der Zirbel-Kiefern-Reliktwälder der Tatra über Kalk (*Swertio perennis-Pinetum cembrae* – 14 Aufnahmen), der *P.-cembra*-Reliktwälder der Tatra (*Vaccinio-Pinetum cembrae typicum* – 69 Aufnahmen) und der Alpen (*Vaccinio-Pinetum cembrae typicum* – 98 Aufnahmen). Arten unterhalb der Stetigkeitsschwelle von II sowie Arten der Stetigkeitsklasse II, jedoch ohne diagnostischen Wert für die Fichten- und Zirbel-Kiefern-Wälder, wurden weggelassen. Dagegen sind Arten der Stetigkeitsklasse I aufgeführt, soweit sie für die Differenzierung der Zirbel-Kiefern-Wälder wesentlich sind. Symbole: C: Stetigkeit (Prozent der Aufnahmen, in welchen das Taxon vorkommt; Stetigkeitsklassen I: 0–20 %, II: 21–40 %, III: 41–60 %, IV: 61–80 %, V: 81–100 %); CR: Deckungsgrad (mittlere Deckung einer Art in den Aufnahmen x 100).

Community number	1		2		3		4		5	
Region	Tatra Mountains									
Plant association	<i>Plagiothecio-Piceetum</i>		<i>Polysticho-Piceetum</i>		<i>Swertio perennis-Pinetum cembrae</i>		<i>Vaccinio-Pinetum cembrae</i>		<i>Vaccinio-Pinetum cembrae</i>	
Av. number of species in relevé	17		48		46		26		26	
Trees and shrubs	C	CR	C	CR	C	CR	C	CR	C	CR
<i>Picea abies</i> A1	V	5833	V	5167	V	1966	V	2591	IV	251
<i>Picea abies</i> A2	I	42	II	444	III	483	III	617	.	.
<i>Picea abies</i> B	II	43	II	56	V	983	V	538	III	72
<i>Picea abies</i> C	III	6	IV	8	III	5	IV	37	II	11
<i>Sorbus aucuparia</i> A1	I	107	III	6	I	.
<i>Sorbus aucuparia</i> A2	II	215	II	19,5	.	.
<i>Sorbus aucuparia</i> B	V	70	V	836	IV	165	V	336	II	65
<i>Sorbus aucuparia</i> C	III	74	IV	166	II	7
<i>Pinus cembra</i> A1	V	2912	V	3565	V	1196
<i>Pinus cembra</i> A2	III	412	II	197	.	.
<i>Pinus cembra</i> B	III	22	IV	124	IV	143
<i>Pinus cembra</i> C	II	3	IV	26	III	29
<i>Larix decidua</i> A1	I	.	III	265	IV	358
<i>Larix decidua</i> B	II	1	III	66
<i>Larix decidua</i> C	I	.	II	8
<i>Betula pubescens</i> A1	I	.	I	80	.	.
<i>Betula pubescens</i> A2	I	51	.	.
<i>Betula pubescens</i> B	I	17	II	80	I	1,6
<i>Betula pubescens</i> C	I	.	I	.	I	.

Community number	1	2	3	4	5
<i>Lonicera nigra</i> B-C	.	IV 33	III 4	I 4	.
<i>Lonicera caerulea</i> B	II 13
<i>Salix silesiaca</i> A2-B-C	.	.	V 150	II 31	.
<i>Pinus mugo</i> B-C	.	I 1	III 965	V 2368	I 108
<i>Daphne mezereum</i> B-C	.	.	III 1	.	.
<i>Rosa pendulina</i> B	.	.	III 3	I 4	.
<i>Ribes petraeum</i> B-C	.	.	II 1	I .	.
<i>Rhododendron ferrugineum</i> B	V 1257
<i>Alnus viridis</i> B-C	I 41
Ch. et Dif. Vaccinio-Pinetum cembrae					
<i>Sphagnum quinquefarium</i>	.	.	II 661	IV 1953	I 11
<i>Vaccinium vitis-idaea</i>	III 45	III 4	V 1518	V 2243	V 360
<i>Rhytidiadelphus triquetrus</i>	.	.	II 304	II 102	II 227
<i>Veratrum lobelianum</i>	.	II 3	III 20	II 5	.
<i>Gentiana punctata</i>	.	.	.	II 59	I .
<i>Cetraria islandica</i>	.	.	I 1	II 28	II 62
<i>Cladonia macroceras</i>	.	.	.	II 1	.
<i>Cladina rangiferina</i>	.	.	I .	I 1	II 47
Ch. et Dif. Swertio perennis-Pinetum cembrae					
<i>Swertia perennis</i>	.	II 2	V 164	.	.
<i>Carex sempervirens</i>	.	.	IV 592	.	I 19
<i>Valeriana tripteris</i>	.	V 36	V 255	.	I .
<i>Saxifraga paniculata</i>	.	.	III 4	.	I .
<i>Scabiosa lucida</i>	.	.	III 3	.	.
<i>Melampyrum herbichii</i>	.	.	III 162	.	.
<i>Campanula polymorpha</i>	.	IV 7	IV 7	I .	.
<i>Tortella tortuosa</i>	.	I 1	III 269	I .	I .
Ch. et Dif. Polysticho-Piceetum					
<i>Polystichum lonchitis</i>	.	III 4	II 2	.	I .
<i>Huperzia selago</i>	I 2	III 6	III 2	III 60	I 4
<i>Mnium spinosum</i>	.	II 29	I .	.	.
<i>Moneses uniflora</i>	.	II 2	I .	.	I .
Ch. Loiseleurio procumbentis-Vaccinieta					
<i>Empetrum hermaphroditum</i>	.	.	I 17	I 18	I 22
<i>Vaccinium gaultherioides</i>	.	.	I 375	I 4	II 107
Ch. Piceion excelsae					
<i>Buckiella undulata</i>	II 3	IV 8	II 54	II 131	I 3
<i>Luzula luzulina</i>	II 3	III 31	.	I 55	I 7
<i>Dryopteris dilatata</i>	V 463	V 143	III 74	V 473	I 2
<i>Homogyne alpina</i>	V 938	V 918	IV 894	IV 518	IV 148
<i>Luzula sylvatica</i>	IV 338	V 142	IV 165	III 165	II 14
<i>Rhytidiadelphus loreus</i>	III 313	V 367	II 143	II 48	I .
<i>Sphagnum girgensohnii</i>	II 3	I 1	I 21	II 533	I 78
Ch. Piceetalia excelsae et Vaccinio-Piceetum					
<i>Deschampsia flexuosa</i>	V 234	IV 34	IV 41	V 665	V 543
<i>Vaccinium myrtillus</i>	V 3729	V 1696	V 3018	V 5667	V 1815
<i>Lycopodium annotinum</i>	II 3	II 29	II 946	III 957	II 7

Community number	1		2		3		4		5	
<i>Calamagrostis arundinacea</i>	I	1	IV	807	IV	1804	I	156	.	.
<i>Clematis alpina</i>	.	.	III	6	IV	39	I	.	.	.
<i>Dicranum scoparium</i>	V	461	V	670	III	661	V	1932	IV	147
<i>Hylocomium splendens</i>	II	128	III	58	III	1401	V	1544	IV	777
<i>Pleurozium schreberi</i>	III	336	V	948	II	326	IV	2008	V	374
<i>Polytrichastrum formosum</i>	IV	4188	V	2973	III	1000	IV	1051	II	165
Ch. Adenostyletalia alliariae et Mulgedio-Aconitetea										
<i>Athyrium distentifolium</i>	III	566	III	86	II	2	II	48	I	.
<i>Polygonatum verticillatum</i>	.	.	V	9	III	127	I	.	I	.
<i>Senecio nemorensis</i>	II	3	V	62	III	1	I	1	I	.
<i>Calamagrostis villosa</i>	II	3	I	28	.	.	IV	1283	III	484
<i>Adenostyles alliariae</i>	.	.	II	3	IV	20	I	.	I	.
Ch. Fagetalia sylvaticae et Carpino-Fagetea sylvaticae										
<i>Prenanthes purpurea</i>	I	1	IV	34	IV	53	II	1	I	.
<i>Astrantia major</i>	.	.	II	2	II	1
<i>Phyteuma spicatum</i>	.	.	IV	7	II	1
Ch. Seslerietalia caeruleae et Elyno-Seslerietea										
<i>Carduus glaucus</i>	II	1	I	.	.	.
<i>Carex firma</i>	III	21	.	.	I	.
<i>Crepis jacquinii</i>	II	38
<i>Dianthus plumarius</i> subsp. <i>praecox</i>	II	2
<i>Festuca tatrae</i>	II	37
<i>Festuca versicolor</i>	II	643
<i>Phyteuma orbiculare</i>	II	2	.	.	I	.
<i>Sesleria tatrae</i>	II	19
<i>Thesium alpinum</i>	II	2

soils. On the other hand, subalpine krummholz vegetation has been classified into the class *Roso pendulinae-Pinetea mugo* Theurillat in Theurillat et al. 1995. Such classification emphasizes the structural and ecological differences between the forest communities along the timberline and non-forest shrubland vegetation above the timberline which is more similar to the arctic-alpine tundra (MUCINA et al. 2016). Furthermore, also LEUSCHNER & ELLENBERG (2017) in the latest edition of the Vegetation Ecology of Central Europe included the *P. cembra* forests in the suballiance *Vaccinio-Piceenion*.

Even though the results of our studies confirm the concept of MYCZKOWSKI (1970) on the distinctiveness of relic *P. cembra* forests from the *Plagiothecio-Piceetum* we point to some differences in the characteristics of this association. In comparison to the original diagnostic species by MYCZKOWSKI (1970), only *Gentiana punctata* retained the same status. The other species, such as *Empetrum hermaphroditum* and *Vaccinium gaultherioides* occur too rarely in the dataset to be considered characteristic for the association. However, as they are almost totally absent in the *Plagiothecio-Piceetum* their presence may be helpful in floristic diagnosis of forests along the timberline. Furthermore, *Athyrium distentifolium* described by MYCZKOWSKI (1970) as a common and diagnostic species in *P. cembra* forests, according to our research occurs there only occasionally (N%: 19%, F: II, CR: 43.5, DR: 10.3), which is another difference to spruce forests where that fern is common (PAWŁOWSKI et al. 1928, MATUSZKIEWICZ 1977) (Table 3).

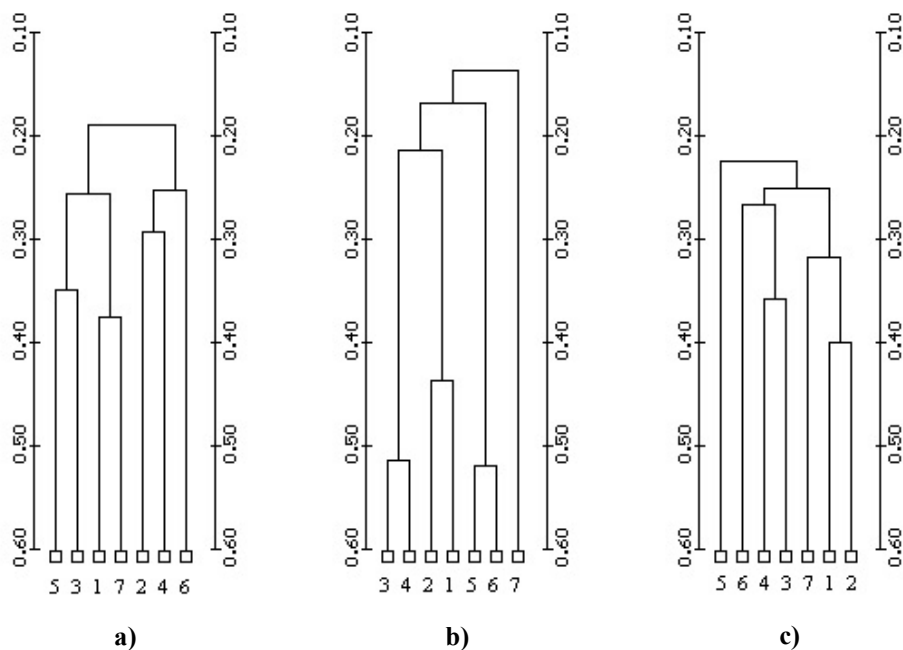


Fig. 3. Similarity analysis of three parameters: A – percentage frequency (F), B – cover ratio (CR), C – dominance ratio (DR) of Tatra relic Swiss stone pine forests (1 – *Vaccinio-Pinetum cembrae typicum*, 2 – *Swertio perennis-Pinetum cembrae*), Tatra upper montane spruce forests (3 – *Plagiothecio-Piceetum*, 4 – *Polysticho-Piceetum*), Tatra subalpine dwarf pine shrubs (5 – *Vaccinio myrtilli-Pinetum mugo*, 6 – *Athyrio distentifolii-Pinetum mugo.*), Alpine Swiss stone pine forests (7 – *Vaccinio-Pinetum cembrae typicum*) based on modified Marczewski and Steinhaus model and UPGMA.

Abb. 3. Ähnlichkeitsanalyse zu drei Parametern von Zirbel-Kiefern-Wäldern der Tatra: A – prozentuale Häufigkeit (F), B – Deckungsgrad (CR), C – Dominanzrelation (DR), basierend auf einer modifizierten Marczewski/Steinhaus-Modellierung und UPGMA.

Differences between the *Vaccinio-Pinetum cembrae* and the *Plagiothecio-Piceetum*, as noted by MYCZKOWSKI (1970), are especially visible in physiognomy and species richness. Broad crowns of *P. cembra* together with characteristic *Larix decidua* are visible from a long distance. Furthermore, a double-layered stand together with admixture of montane broad-leaved species make them even more distinctive from usually single-layered and monospecific spruce forests. Another structural feature in which relic *P. cembra* forest differ from the *Plagiothecio-Piceetum* is the well-developed shrub layer, which consists mostly of subalpine species representing *Pinion mugo* (Fig. 2d). In addition, the ground layer together with the moss layer stands out at first glance by (1) abundance of *Vaccinium vitis-idaea*, which is a rather rare plant in typical spruce forests, (2) presence of *Sphagnum quinquefarium* – a taxon that does not occur in the *Plagiothecio-Piceetum* and (3) relative rarity or even lack of *Buckiella undulata*, a species characteristic for Western Carpathian spruce forests. In addition to that, in the relic *P. cembra* forest we recorded some of the subalpine plant species as well as lichens (mostly *Cladonia* spp. and *Cetraria islandica*), which are almost absent in spruce forests (Table 3, Supplement S2).

Furthermore, it is worth emphasizing the *Vaccinio-Pinetum cembrae juncetosum trifidi*, a new subassociation of *P. cembra* forests. Hitherto several subassociations of *P. cembra* forests on granite bedrock have been described (MAYER 1974, ELLENBERG 1978, WOJTERSKA et al. 2004, WILLNER & GRABHERR 2007). Nonetheless, WILLNER & GRABHERR (2007), in a synthesis of Austrian plant communities, distinguished three subassociations of the *Vaccinio-Pinetum cembrae* from the Alps: *typicum*, *alnetosum viridis* and *nardetosum*. However, the latter two have provisional status (WILLNER & GRABHERR 2007). In addition to that, WOJTERSKA et al. (2004) described from the Roztoka Valley in the Tatra a subassociation called *Larici-Pinetum cembrae sphagnetosum* Wojterska, Wojterski, Szwed et Piaszyk 2004. A similar subassociation was described from the Alps (MAYER 1974). However, the results of our study did not reveal such a subassociation, even though five relevés were made in the Roztoka Valley. Nonetheless, *Sphagnum* spp. mosses are abundant in the relic Swiss stone pine forests, along with being distinguished as characteristic *Sphagnum quinquefarium*. Especially high values of cover of *Sphagnum* spp. mosses were detected in the variants: *Cladonia* spp. and *Gymnocarpium dryopteris* and maybe they are equivalent to the *Larici-Pinetum cembrae sphagnetosum*. However, on the basis of numerical analysis we prefer to classify variants, not a subassociation.

An interesting aspect of this study was finding *P. cembra* forests on limestone and dolomite bedrock, *Swertio perennis-Pinetum cembrae*, which has not been so far documented from the Tatra Mountains (HOLEKSA & SZWAGRZYK 2004, MATUSZKIEWICZ 2008, MRÓZ et al. 2012). Analogous plant communities were so far known from the Alps as *Rhododendro hirsuti-Pinetum cembrae* Bojko 1931 (WILLNER & GRABHERR 2007). Even though both associations seem to occupy a similar niche, their floristic composition differ enough to consider separate syntaxonomical units. Diagnostic species of the *Rhododendro hirsuti-Pinetum cembrae* are mostly alpine plants that do not occur in the Tatra, such as *Rhododendron hirsutum*, *Veratrum album* and *Erica carnea* (WILLNER & GRABHERR 2007). On the other hand, the characteristic and name-giving *Swertia perennis* is totally absent in the alpine calcicolous *P. cembra* forests (according to data presented in WILLNER & GRABHERR 2007).

Furthermore in the *Swertio perennis-Pinetum cembrae*, apart from the species typical for the *Vaccinio-Piceetea*, we found species representing the *Carpino-Fagetea sylvaticae*. A similar phenomenon has been described from the calcicolous upper montane spruce forests (*Polysticho-Piceetum*; MATUSZKIEWICZ et al. 2007, MATUSZKIEWICZ 2008) (Table 3). However, it is worth mentioning that in some parts of such forests, probably due to acidic humus accumulation, the herb layer did not differ from that in the *P. cembra* forests on granite bedrock. Therefore, some of the relevés on dolomite or limestone bedrock were classified as *Vaccinio-Pinetum cembrae typicum* (relevés 29, 51, 52).

Except in the Tatra and the Alps, *P. cembra* forests occur also in the Eastern and Southern Carpathians. Botanists described from that region the association called *Pino cembrae-Piceetum* Chifu et al. 1984 (SANDA et al. 2008). This relic occurrence of *P. cembra* in Europe resembles taiga forests with Siberian stone pine (*Pinus cembra* subsp. *sibirica*) from Central Siberia (MYCZKOWSKI 1969). KUNEŠ et al. (2008) found evidence on the basis of pollen data that the vegetation (including *P. cembra* forests) in the Central-Eastern European mountain chains during the last stages of the Ice Age was similar to that in present-day Central-Southern Siberian mountains. In addition to that, they stressed the similarities of the current flora between these two regions, especially the share of Euro-Siberian species (KUNEŠ et al. 2008). In light of these results, the combined syntaxonomical and ecological

comparison of Central European (Alpine and Carpathian) *P. cembra* forests and Siberian stone pine taiga representing *Vaccinio-Pinetalia sibiricae* Zhitlukhina et Alimbekova 1987 (ANENKHONOV & CHYTRÝ 1998) or *Piceo obovatae-Pinetalia sibiricae* Ermakov 2013 (MUCINA et al. 2016) seems to be appealing.

Erweiterte deutsche Zusammenfassung

Einführung – Zirbel-Kiefern-Reliktwälder gehören zu den am wenigsten untersuchten Pflanzengesellschaften der West-Karpaten. Dort sind Zirbel-Kiefer (*Pinus cembra*) und Lärche (*Larix decidua* subsp. *decidua*) nur in der Tatra autochthon. Pflanzensoziologische Erhebungen an den Zirbel-Kiefern-Wäldern der Tatra wurden in den 1960/70er Jahren durch Myczkowski durchgeführt und in einem Teilgebiet durch WOJTERSKA et al. (2004). Diese Untersuchungen mündeten in die Beschreibung einer Assoziation der Zirbel-Kiefern-Reliktwälder der Tatra, *Cembro-Piceetum*, beziehungsweise nach WOJTERSKA et al. (2004), *Larici-Pinetum cembrae*. Der syntaxonomische Status blieb indes strittig wegen unzureichender Datenbasis. So stufte MATUSZKIEWICZ (2008) alle Zirbel-Kiefern-Bestände als eine lokale Ausprägung der hochmontanen Fichtenwälder ein (*Plagiothecio-Piceetum*). Ziel der vorliegenden Studie ist es daher, den syntaxonomischen Status der Zirbel-Kiefern-Wälder der Tatra zu klären unter Einbeziehung der bisher nicht untersuchten Vorkommen auf Kalkgestein und in der Westlichen Tatra (polnisch *Tatry Zachodnie*, slowakisch *Západné Tatry*).

Untersuchungsgebiet – Unsere Untersuchungen wurden in der Tatra durchgeführt, die anteilig zu Polen und der Slowakei gehört. Die Tatra ist das höchste Gebirgsmassiv der Karpaten (höchste Erhebung: Gerlach, 2655 m ü.M.). Teile der polnischen und slowakischen Tatra sind Nationalparks der IUCN-Kategorie II, zudem UNESCO-Biosphärenreservat und als SPA und SAC zum europäischen Schutzgebietsnetz Natura 2000 gehörig. Zirbel-Kiefern-Reliktwälder kommen in der Tatra zwischen 1300 und 1600 m ü.M. an der Waldgrenze vor. Die anstehenden Gesteine in diesen Höhenlagen sind Granit, Kalk, Dolomit und Quarzsandstein, die daraus entstandenen Böden Podsol, Rendzina und Ranker. Zirbel-Kiefern-Wälder wachsen dort bei einer Jahresdurchschnittstemperatur um +3 °C und mittleren Jahresniederschlagssummen von 1400 mm.

Methoden – Wir fertigten 108 Vegetationsaufnahmen nach der Braun-Blanquet-Methode im gesamten Verbreitungsgebiet von *P. cembra* in der Tatra an. Zum Vergleich verwendeten wir außerdem veröffentlichte Aufnahmen von hochmontanen Fichtenwäldern und Kalk-Fichtenwäldern der Tatra (*Plagiothecio-Piceetum*, *Polysticho-Piceetum*; Daten aus MATUSZKIEWICZ et al. 2007), von subalpinem Latschen-Krummholz der Tatra (*Vaccinio myrtilli-Pinetum mugo*, *Athyrio distentifolii-Pinetum mugo*; Daten aus SZCZYGIELSKI 2001) sowie von Zirbel-Kiefern-Wäldern der Alpen (*Vaccinio-Pinetum cembrae*; Daten der Österreichischen Vegetationsdatenbank, WILLNER et al. 2012).

Die Felddaten wurden mittels UPGMA klassifiziert; Ähnlichkeitsmatrizes wurden mittels des modifizierten Marczewski-Steinhaus-Modells berechnet. Jede Aufnahme wurde 4-fach klassifiziert, mit jeweils unterschiedlichen Transformationen der Ausgangsmatrix. Die syntaxonomische Zuordnung jeder Aufnahme basierte auf Berechnungen eines Index der pflanzensoziologischen Übereinstimmung (IPA). Charakter- und Differenzialarten wurden aufgrund von Stetigkeit (N %), Treue (F), Deckungsgrad (CR) und Dominanzverhältnissen (DR) bestimmt. Die syntaxonomische Absicherung basiert auf Ähnlichkeitsanalysen (mit den Variablen N %, CR und DR) zwischen den ermittelten Syntaxa und den nächstverwandten Pflanzengesellschaften der Tatra und der Alpen.

Ergebnisse und Diskussion – Wir unterschieden zwei Assoziationen der Zirbel-Kiefern-Reliktwälder der Tatra – (1) *Vaccinio-Pinetum cembrae* (Pallmann & Haffter 1933) Oberdorfer 1962 und (2) über Kalk das *Swertio perennis-Pinetum cembrae* ass. nov., ferner eine Gruppe von Aufnahmen mit unklarem syntaxonomischen Status. Diagnostisch für das *Vaccinio-Pinetum cembrae* sind die Charakterarten *P. cembra*, *Gentiana punctata*, *Sphagnum quinquefarium* und *Cladonia macroceras* sowie die Differenzialarten *Larix decidua*, *Sorbus aucuparia* var. *glabrata*, *Salix silesiaca*, *Betula*

pubescens subsp. *carpatica*, *Veratrum lobelianum*, *Vaccinium vitis-idaea*, *Rhytidiadelphus triquetrus* und *Cetraria islandica*. Das *Vaccinio-Pinetum cembrae* wird in zwei Subassoziationen aufgeteilt, subass. *typicum* mit drei Varianten (var. *Larix decidua*, var. *Cladonia* spp. und var. *Gymnocarpium dryopteris*) sowie subass. *juncetosum trifidi* subass. nov. Diagnostische Arten des *Swertio perennis-Pinetum cembrae* sind *P. cembra* und *Swertia perennis* sowie die Differenzialarten *Carex sempervirens*, *Valeriana tripteris*, *Saxifraga paniculata*, *Scabiosa lucida*, *Melampyrum herbichii*, *Campanula polymorpha*, *Sphagnum quinquefarium* und *Tortella tortuosa*. Bei dieser Assoziation lassen sich zwei Varianten unterscheiden, var. *Valeriana tripteris* and var. *Carex sempervirens*.

Ähnlichkeitsanalysen bestätigen die Eigenständigkeit der beiden Assoziationen und ihre Trennung vom *Plagiothecio-Piceetum*, sowie die Identität des *Vaccinio-Pinetum cembrae* der Alpen und der Tatra als bloße geographische Varianten in einer Assoziation. Ein höheres Maß an Ähnlichkeit zwischen Zirbel-Kiefern-Wäldern und hochmontanen Fichtenwäldern gegenüber Latschen-Krummholz legt nahe, erstere zum Unterverband *Vaccinio-Piceetion* statt zum *Rhododendro-Vaccinienion* beziehungsweise *Pinion mugo* zu stellen.

Ein interessanter Aspekt unserer Studie war die Entdeckung des *Swertio perennis-Pinetum cembrae*, Zirbel-Kiefern-Wäldern über Kalk- und Dolomitgestein, die bisher aus der Tatra noch nicht beschrieben worden waren. Eine analoge Assoziation der Alpen ist das *Rhododendro hirsuti-Pinetum cembrae*. Trotz offenbar ähnlicher ökologischer Nische rechtfertigen die floristischen Unterschiede ihre Einstufung als getrennte Assoziationen.

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Supplements

Supplement S1. Classifications of 108 relevés made in the relic Swiss stone pine forests and adjacent forests in the Tatra Mountains, based on the four variants of transformation of initial data matrix: A – binary, B – “neutral”, C – “neutral” (layers B, C, D), D – average percentage of coverage.

Beilage S1. Dendrogramm der UPGMA-Klassifikation der 108 Vegetationsaufnahmen von Zirbel-Kiefern- und angrenzenden Wäldern der Tatra, auf vier Transformationsvarianten der ursprünglichen Datenmatrix basierend: A – binär, B – “neutral”, C – “neutral” (Schichten B, C, D), D – mittlere prozentuale Deckung.

Supplement S2. Relic Swiss stone pine forests *Vaccinio-Pinetum cembrae* (Pallmann & Haffter 1933) Oberdorfer 1962 in the Tatra Mountains, including *Vaccinio-Pinetum cembrae juncetosum trifidi* subass. nov. hoc loco, holotypus: relevé 82.

Beilage S2. Zirbel-Kiefern-Reliktwälder *Vaccinio-Pinetum cembrae* (Pallmann & Haffter 1933) Oberdorfer 1962 in der Tatra. Holotypus des *Vaccinio-Pinetum cembrae juncetosum trifidi* ass. nov. ist Aufnahme 82.

Supplement S3. Relic calcicolous Swiss stone pine forest of the Tatra Mountains *Swertio perennis-Pinetum cembrae* ass. nov. hoc loco, holotypus: relevé 33.

Beilage S3. Zirbel-Kiefern-Reliktwälder der Tatra über Kalk. Holotypus des *Swertio perennis-Pinetum cembrae* ass. nov. ist Aufnahme 33.

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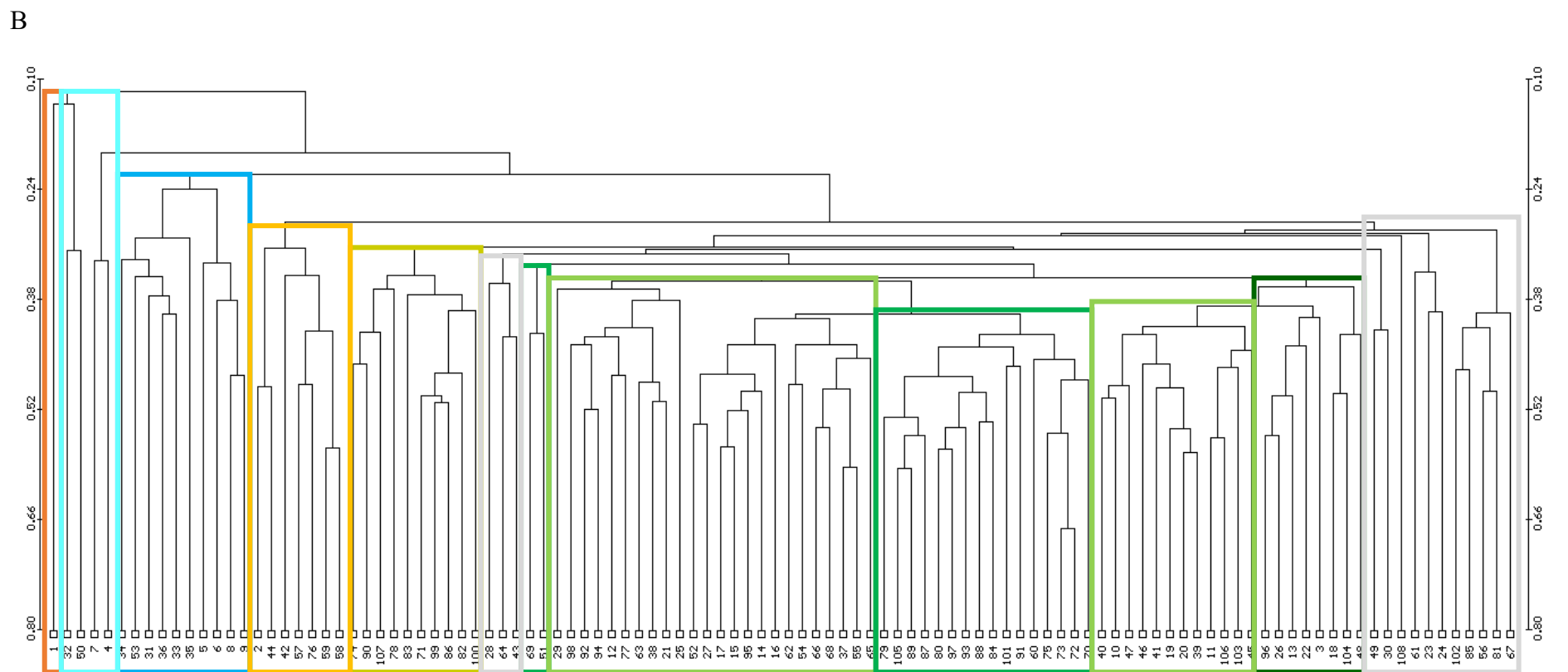
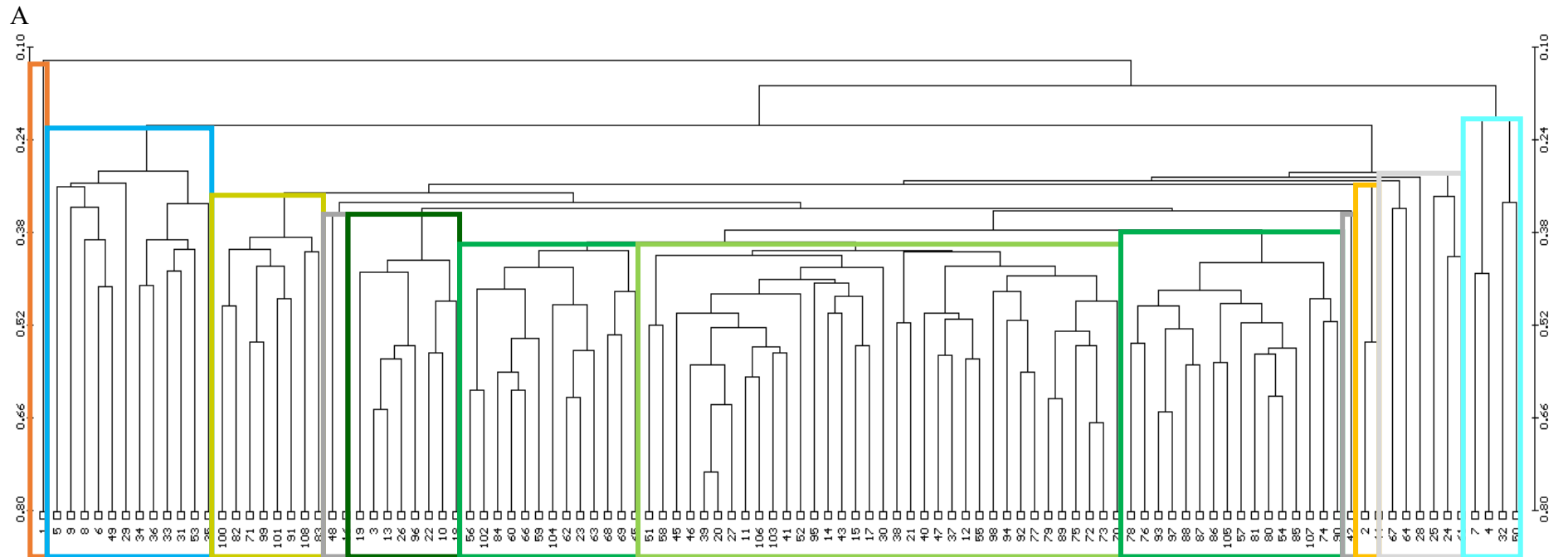
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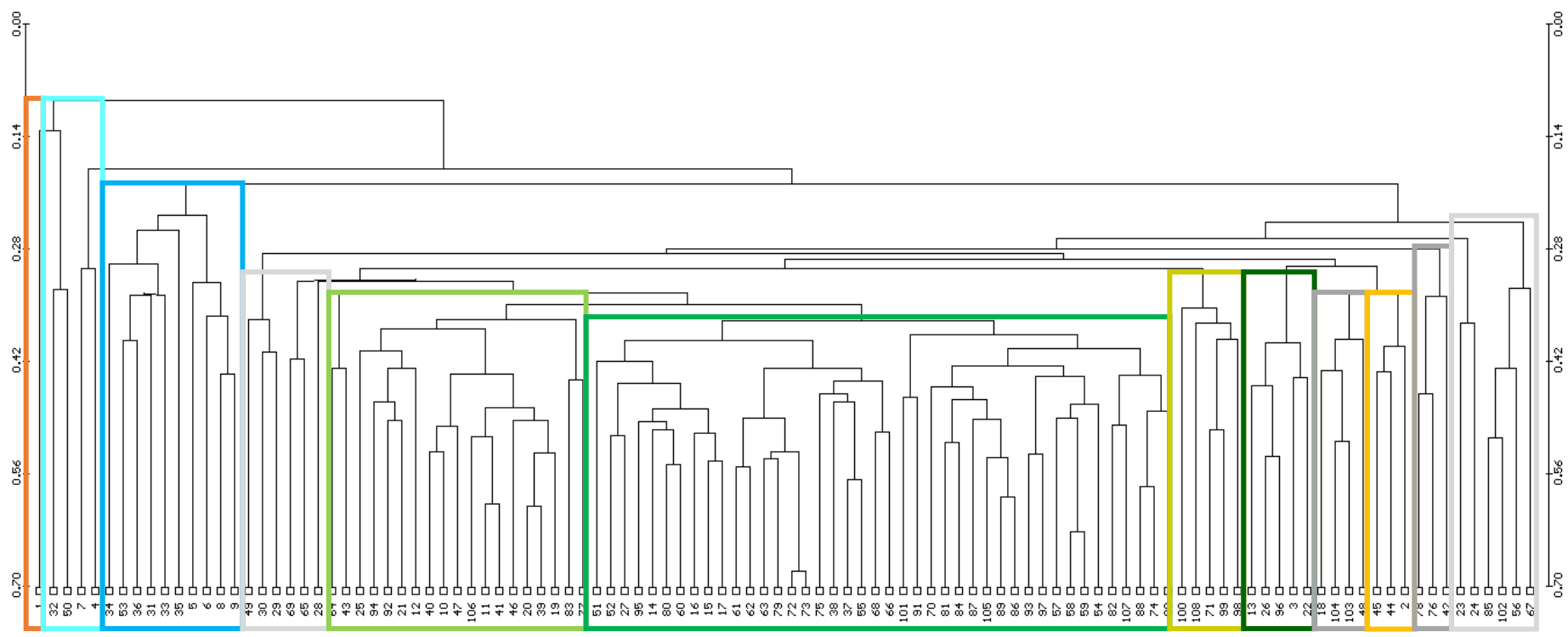
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Supplement S1. Classifications of 108 relevés made in the relic Swiss stone pine forests and adjacent forests in the Tatra Mountains, based on the four variants of transformation of initial data matrix: A – binary, B – “neutral”, C – “neutral” (layers B, C, D), D – average percentage of coverage. Dendrograms made according to the UPGMA (SNEATH & SOKAL 1973). Distinguished syntaxa: □ - *Swertio perennis-Pinetum cembrae* var. *Carex sempervirens*, □ - *S.p-P.c.* var. *Valeriana tripteris*, □ - *Vaccinio-Pinetum cembrae* var. *Larix decidua*, □ - *V.-P.c.* var. *Cladonia* spp., □ - *V.-P.c. juncetosum trifidi*, □ - *P. cembra* woodland fragments, □ - *P. cembra* woodland fragments / *Plagiothecio-Piceetum*, □ - *Plagiothecio-Piceetum*, □ - artificial *Pinus cembra* woodlot.

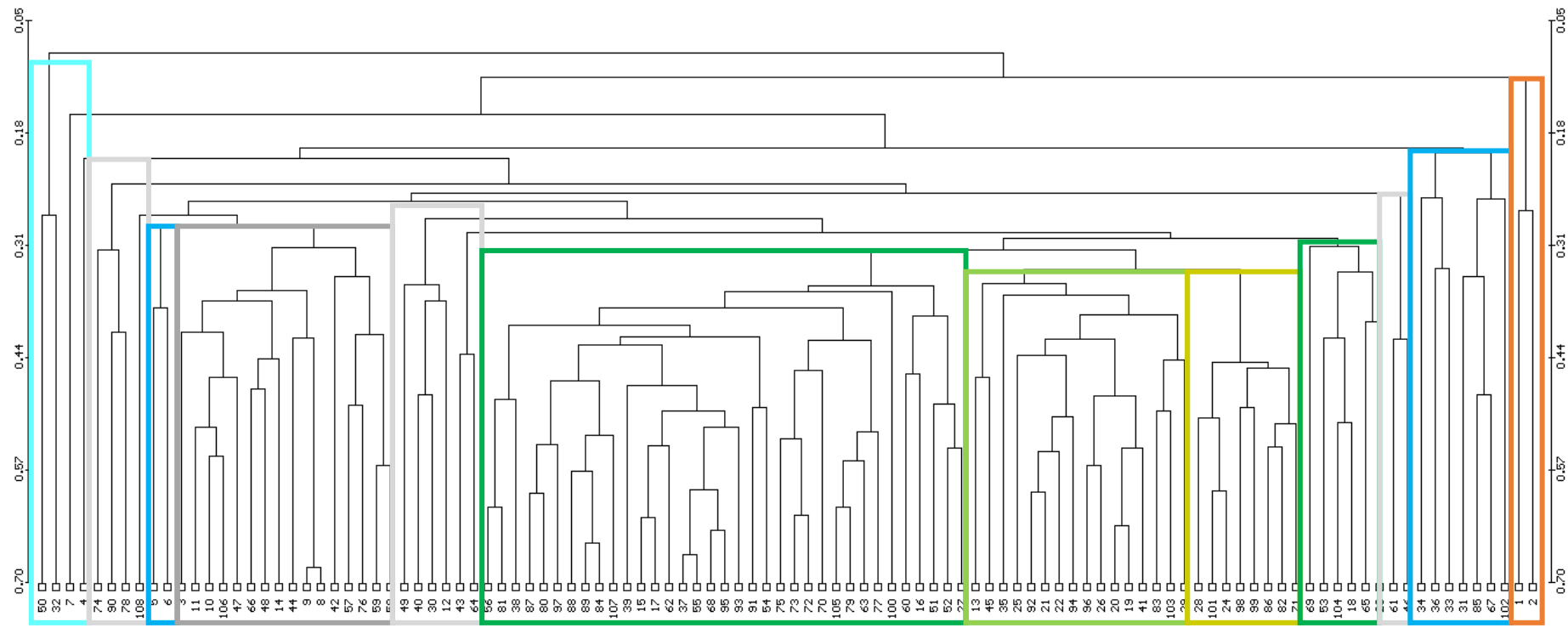
Beilage S1. Dendrogramm der UPGMA-Klassifikation (nach SNEATH & SOKAL 1973) der 108 Vegetationsaufnahmen von Zirbel-Kiefern- und angrenzenden Wäldern der Tatra, auf vier Transformationsvarianten der ursprünglichen Datenmatrix basierend: A – binär, B – “neutral”, C – “neutral” (Schichten B, C, D), D – mittlere prozentuale Deckung. Unterschiedene Syntaxa: □ - *Swertio perennis-Pinetum cembrae* var. *Carex sempervirens*, □ - *S.p-P.c.* var. *Valeriana tripteris*, □ - *Vaccinio-Pinetum cembrae* var. *Larix decidua*, □ - *V.-P.c.* var. *Cladonia* spp., □ - *V.-P.c. juncetosum trifidi*, □ - *P. cembra*-Waldfragmente, □ - *P. cembra* -Waldfragmente / *Plagiothecio-Piceetum*, □ - *Plagiothecio-Piceetum*, □ - künstliches *Pinus cembra*-Waldstück.



C



D



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