

Sphagnum – *Polytrichum* turf hummocks in the Western Carpathians

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Abstract. Turf hummocks co-dominated by *Polytrichum strictum* and *Sphagnum capillifolium* arise in different ecosystems – alpine heaths, raised bogs and minerotrophic mires. They share common features – with a conjoint origin, ombrotrophy and their separation from substrata. Many studies have looked at turf hummocks, but the question of whether to classify the turf hummocks separately or not is still unsolved. The study area was within the Western Carpathians, from mires in the bottoms of basins, rising to the alpine belt where 79 phytocoenological relevés were submitted for numerical classification. The standard procedures of the Zürich-Montpellier School were used and the CANOCO 4.5 package served for all numerical analysis. The new association *Vaccinio vitis-idaei* – *Sphagnetum capillifolii* consisting of two subassociations: *typicum* and *eriophoretosum vaginati* is suggested. We propose to include the turf hummock communities developed in the mires and fens within the alliance *Oxycocco* – *Empetrium hermaphroditum*. The formation of turf hummocks is closely related to their decomposition, and is independent of substratum. They are raised above the influence of ground water and head towards more or less similarity in chemistry and in the floristical composition, i. e. co-dominance of *Polytrichum strictum* and *Sphagnum capillifolium*. The turf hummocks communities bear distinct azonal features.

Key words: Turf hummocks, syntaxonomy, mires, numerical classification, ordination, Western Carpathians

Introduction

Sphagnum is the most important peat-forming genus, despite the fact, that species of section *Sphagnum* have low productivity figures (Gunnarsson 2005), while net primary production is a key regulator of ecological processes (Thompson *et al.* 1996; Vitt *et al.* 2001). Many *Sphagnum* species have been found to be quite resistant to microbial decomposition compared with most vascular plant species (Aerts *et al.* 1999, Glime 2007). For

hummocks to develop, certain conditions must be present; most importantly, there must be a reduction in flooding and sedimentation. Turf hummocks are found exclusively in sites without tree or shrub canopy (Gill 1973). The plant communities under a *Pinus mugo* canopy, which are rich in *Sphagnum*, have been analysed by Šibík *et al.* (2008). Despite the presence of *Sphagnum capillifolium* and *Polytrichum strictum*, turf hummocks are absent. Apparently, the overstorey of *Pinus mugo* is an obstacle for turf hummocks developing and the development of chionophyllous turf hummocks is limited by the shortened vegetation period (Šibík *et al.* 2006). An important ecological condition seems to be that the hummocks form only where no running water is present, sustained only by precipitation (Szweykowski and Buczkowska 2000).

Turf hummocks have a typical knob-like shape covered by vegetation. The term turf hummock is used here to describe the *Polytrichum strictum* – *Sphagnum capillifolium* (*Sphagnum rubellum* respectively) association in the moss-turf formation. These two mosses either individually (*Sphagnum*) or more commonly in association, accumulate organic matter frequently up to 0.3 - 0.7m in depth in different ecosystems – alpine heaths, raised bogs or rich fens.

Sphagnum rubellum has not been recognized as a species in several bryophyte floras, instead it has been treated as a variety or ecotype of *Sphagnum capillifolium* (Gunnarsson 2005). Thus, in some cases *Sphagnum capillifolium* named in literature reviews may include *Sphagnum rubellum*. Due to these differences in taxonomic status in phytosociological research, *Sphagnum capillifolium* was merged with *Sphagnum rubellum* in the synoptic table.

Seppala (2002) considers hummock development as an indicator of a general cooling trend, developing mostly during the second half of the Holocene. Earth hummocks are a circumpolar phenomenon found in northern Europe, Greenland, Iceland and in many permafrost regions of northern Canada such as the subarctic forest of the Mackenzie Valley, the Yukon, the western and central Arctic and on the Arctic islands. In contrast, there have been few reports from alpine regions of North America (Scotter and Zoltai 1982). Also, *Polytrichum* dominated hummocks occur in Antarctica (Fenton and Smith 1982). Earth hummocks are nearly always associated with permafrost, whereas in non permafrost, are supposed to be fossil forms (Scotter and Zoltai 1982, Szweykowski and Buczkowska 2000), their formation being related to cryoturbation (Tarnocai and Zoltai 1978). The turf hummocks in the West Carpathians ecosystems differ from these

earth hummocks - they are found in a non-permafrost environment and cannot be regarded as fossil forms. They consist of turf, the majority of them are active, juvenile or incipient. They are rare and only locally may they cover relatively large areas and become a unique feature in the vegetation. In the Polish part of the Tatra Mts, the hummocks are most typically formed on the North and West facing slopes in all mountains, but most frequently in its western parts (Cykowska 2006, 2009, 2011). These formations may occur in areas 10 to 100 meters across which were not forming separate hummocks. Szweykowski and Buczkowska (2000) interpret such cases as peat bogs occurring on slopes. Turf hummocks harbour a rich variety of rare and relic species of the hepatic flora, e.g. *Barbilophozia binsteadii* (Szweykowski 1960). Cykowska (2006, 2009, 2011) found 50 species of rare and noteworthy species of hepatics such as *Barbilophozia atlantica*, *B. binsteadii*, *B. kunzeana*, *Calypogea sphagnicola*, *Cephalozia convivens* growing on the hummocks. Also Klama (2004) in monograph of liverworts of Babia Góra National Park published a list of liverworts growing on *Sphagnum-Polytrichum* hummocks in alpine level of Mt Babia Góra.

This peat is composed almost entirely of two turf forming mosses – *Polytrichum strictum* and *Sphagnum capillifolium* (*S. rubellum* respectively). The hummocks co-dominated by *Polytrichum strictum* and *Sphagnum capillifolium* are not confined to alpine heaths and raised bogs as minerotrophic fens create these unusual structures as well.

The question of whether or not to classify the turf hummocks separately is still unsolved. The aims of this paper are a) to discuss the convergent development turf hummocks communities co-dominated by *Sphagnum capillifolium* and *Polytrichum strictum* develop in different ecosystems; b) to study the transition to ombrotrophic conditions and analyse the ombrotrophic turf hummock communities with respect to ecological conditions; c) to suggest taxonomical classification of the syntaxa.

Phytocoenologists have often treated the turf hummocks communities in terms of their neighbouring vegetation. Dúbravcová *et al.* (1976) included turf hummock communities in the association *Empetro – Vaccinietum* Sill. 1933 as variant with *Sphagnum nemoreum*, alliance *Loiseulerio – Vaccinion uliginosi* Krajina 1933. Šibík *et al.* (2006) created a new association for peat hummocks communities: *Sphagno capillifolii – Empetretum nigri* within the alliance *Vaccinion myrtilli* Krajina 1933 dominated by peat moss.

Dítě *et al.* (2007) did not mention any similar plant communities in a list of Slovak plant mire associations, likewise in Polish phytosociological literature (Matuszkiewicz 2006). Such structures represent a rare phenomenon among the Carpathian mires (Hájková and Hájek 2004) and comprehensive phytocoenological material is lacking. The purpose of this paper is fill this gap in the knowledge.

Material and Methods

Data set

The survey is based on the analysis of 79 phytocoenological relevés of turf hummocks where *Sphagnum capillifolium* and *Polytrichum strictum* are co-dominant.

49 relevés were considered as mature hummocks, whereas the remainder were rated as newly formed or disintegrated hummocks. The relevés were sampled in the Western Carpathians; throughout the alpine belt of the West Tatra Mts and High Tatra Mts (Slovakian and Polish sides), in the mires of montane and alpine belt of the Tatra Mts (Slepé pleso raised bog, Christlová raised bog, Žabia Bielowodská dolina valley, Kolová dolina valley, Rakytovské pliesko raised bog), the Popradská kotlina basin (Belianske lúky meadows), the Liptovská kotlina basin (mire Záhatia), Spišská Magura (mire Velké Osturmianske jazero lake), Velká Fatra Mts (mire near Rojkov), Slovenský raj paradise (mire near Dobšínská Ladová Jaskyňa village) and in Muránska planina plateau (mire along Havraník stream). The evaluation was carried out from data collected over the period 2004 – 2009, and also included were six relevés collected by Dúbravcová *et al.* (1976).

All the relevés were taken following standard procedures of the Zürich-Montpellier School (Braun-Blanquet 1964, Westhoff and Van den Maarel 1978), using the modified 9-degree Braun-Blanquet's sampling scale (Barkman *et al.* 1964) transformed into the ordinal scale of Van den Maarel (1979) and stored in the TURBOVEG data-base (Hennekens and Schaminée 2001). The data were exported into JUICE 7.0 software for analysis (Tichý and Holt 2006). Shrub- and herb-layer records for any one taxon were merged. Numerical classification of the 79 relevés was performed using the statistical tool for plant ecology MULVA-5 (Wildi and Orlóci 1996).

The nomenclature of bryophytes follows Kubínská and Janovicová (1998) and Marhold (1998) for vascular plants.

The descriptions of new communities follows the Code of Phytocoenological nomenclature (Weber *et al.* 2000). The subspecies in the tables, given without the species name are marked with asterisks (*). The geographical coordinates are recorded in the system WGS 84 Garmin eTrex Vista device.

Data analysis

CANOCO 4.5 for Windows package (Ter Braak and Šmilauer 2002) was used for all statistical analysis. Since the length of the first gradient in the log report was > 4, we used the unimodal methods – DCA, CCA (Ter Braak and Šmilauer 2002). For ecological interpretation of the ordination axes, weighted Ellenberg's indicator values of plants (Ellenberg *et al.* 1992) were plotted onto DCA ordination diagram as supplementary environmental variables (L – light, T – temperature, C – continentality, M – moisture, R – reaction, N – nitrogen).

The statistical significance of the explanatory (environmental) variables in canonical methods were determined by Monte Carlo permutation tests. Explanatory variables were tested separately (partial tests). For ordination analysis we used ordinal species data without transformation.

Chemistry

Water sampling for chemical analysis was conducted by catotelm extraction from peat substratum in drainage hollows.

Aqueous aluminium was determined spectro-

photometrically using pyrocatechin violet (Driscoll 1984) and ammonium nitrate using a spectrophotometric method with Nessler reagent (Horáková *et al.* 1989). Chlorides, sulphates and nitrates were determined using capillary zonal electrophoresis, using device EA 101, with buffer solution 7 mM succinic acid + 0.5 mM BTP (bis-tris-propen) + 5% PVP (polyvinylpyrrolidone) + 0.1 % MHEC (methylhydroxyethylcellulose). Cations (K^+ , Na^+ , Ca^{2+} , Mg^{2+}) were determined using isotachophoretic methods in the first colony, using device ZKI 02. The following electrolytes were used:

LE: $10\text{ mmol l}^{-1} NH_4OH + CH_3COOH + 30\%$ PEG (polyethylene glycol) + 0.1% HEC (hydroxyethylcellulose).

TE: 8 mmol l^{-1} tetraethylammonium perchlorate. Conductivity was determined using device OK-104, pH by pH-meter WTW pH 91.

Results

Numerical classification

For cluster analysis, data were exported in ordinal scale without transformation, using correlation coefficient as resemblance function and

Group No. Number of relevés			
	A	B	C
Diagnostic species	14	16	19
<i>Vaccinium vitis-idaea</i> (char., E ₁)	86 ^{39.3}	31 ^{...}	58 ^{...}
<i>Sphagnum capillifolium</i> incl.			
<i>S. rubellum</i> (dom., E ₀)	100 ^{...}	100 ^{...}	100 ^{...}
<i>Polytrichum strictum</i> (dom., E ₀)	100 ^{...}	100 ^{...}	100 ^{...}
Differential species			
<i>Vaccinium myrtillus</i>	100 ^{81.3}	19 ^{...}	11 ^{...}
<i>Avenella flexuosa</i>	86 ^{84.4}	6 ^{...}	...
<i>Juncus trifidus</i>	79 ^{84.2}
<i>Homogyne alpina</i>	64 ^{68.0}	6 ^{...}	...
<i>Oreochloa disticha</i>	64 ^{73.9}
<i>Eriophorum vaginatum</i>	...	100 ^{100.0}	...
<i>Oxycoccus palustris</i> incl.			
<i>O. microcarpus</i>	...	75 ^{65.1}	21 ^{...}
<i>Potentilla erecta</i>	95 ^{96.1}
<i>Drosera rotundifolia</i>	...	25 ^{...}	53 ^{43.2}
<i>Molinia caerulea</i>	68 ^{76.9}
<i>Carex nigra</i>	63 ^{73.0}
Other species			
<i>Succisa pratensis</i>	47 ^{61.2}
<i>Frangula alnus</i>	42 ^{57.1}
<i>Pinus sylvestris</i>	42 ^{57.1}
<i>Equisetum palustre</i>	42 ^{57.1}
<i>Cirsium palustre</i>	37 ^{52.9}
<i>Sphagnum magellanicum</i> (E ₀)	...	38 ^{53.5}	...
<i>Pinus mugo</i>	...	38 ^{53.5}	...
<i>Betula pendula</i>	32 ^{48.5}
<i>Picea abies</i>	32 ^{48.5}
<i>Carex paniculata</i>	32 ^{48.5}
<i>Gentiana punctata</i>	21 ^{22.6}	12 ^{2.7}	...
<i>Pleurozium schreberi</i> (E ₀)	36 ^{52.0}
<i>Cetraria islandica</i> (E ₀)	36 ^{52.0}
<i>Campanula alpina</i>	36 ^{52.0}
<i>Luzula alpino pilosa</i>	36 ^{52.0}
<i>Calluna vulgaris</i>	...	19 ^{21.4}	11 ^{1.8}

<i>Menyanthes trifoliata</i>	26 ^{43.9}
<i>Filipendula ulmaria</i>	26 ^{43.9}
<i>Vaccinium gaultherioides</i>	29 ^{45.9}
<i>Ligusticum mutellina</i>	29 ^{45.9}
<i>Agrostis rupestris</i>	29 ^{45.9}
<i>Festuca supina</i>	29 ^{45.9}
<i>Polytrichum alpinum</i> (E ₀)	29 ^{45.9}
<i>Carex limosa</i>	...	25 ^{42.6}	...
<i>Cephalozia lunulifolia</i> (E ₀)	...	25 ^{42.6}	...
<i>Carex rostrata</i>	...	25 ^{42.6}	...
<i>Galium palustre</i>	21 ^{38.9}
<i>Lysimachia vulgaris</i>	21 ^{38.9}
<i>Epipactis palustris</i>	21 ^{38.9}
<i>Calamagrostis villosa</i>	21 ^{39.2}
<i>Hieracium alpinum</i>	21 ^{39.2}
<i>Huperzia selago</i>	21 ^{39.2}
<i>Cetraria cucullata</i> (E ₀)	21 ^{39.2}
<i>Alectoria ochroleuca</i> (E ₀)	21 ^{39.2}
<i>Scheuchzeria palustris</i>	...	19 ^{36.5}	...
<i>Gymnocolea inflata</i> (E ₀)	...	19 ^{36.5}	...
<i>Tomentypnum nitens</i> (E ₀)	16 ^{33.3}
<i>Aulacomnium palustre</i> (E ₀)	16 ^{33.3}
<i>Parnassia palustris</i>	16 ^{33.3}
<i>Galium uliginosum</i>	16 ^{33.3}
<i>Ligularia sibirica</i>	16 ^{33.3}
<i>Angelica sylvestris</i>	16 ^{33.3}
<i>Carex panicea</i>	16 ^{33.3}
<i>Lathyrus pratensis</i>	16 ^{33.3}
<i>Sphagnum girgensohnii</i> (E ₀)	14 ^{31.6}
<i>Pulsatilla scherfelii</i>	14 ^{31.6}
<i>Avenula versicolor</i>	14 ^{31.6}
<i>Dicranum scoparium</i> (E ₀)	14 ^{31.6}
<i>Wamstorffia fluitans</i> (E ₀)	...	12 ^{29.5}	...
<i>Carex pauciflora</i>	...	12 ^{29.5}	...
<i>Sphagnum fallax</i> (E ₀)	...	6 ^{8.9}	5 ^{5.2}
<i>Juncus articulatus</i>	11 ^{27.0}
<i>Briza media</i>	11 ^{27.0}
<i>Carex flava</i>	11 ^{27.0}
<i>Crepis paludosa</i>	11 ^{27.0}
<i>Salix cinerea</i>	11 ^{27.0}
<i>Festuca rubra</i>	11 ^{27.0}
<i>Pyrola rotundifolia</i>	11 ^{27.0}

Table 1. Shortened synoptic table of turf hummocks co-dominated by *Sphagnum capillifolium* and *Polytrichum strictum* with percentage frequency and modified fidelity index ($\phi - \Phi$ – coefficient). The taxa are sorted according to their fidelity (ϕ coefficient $\times 100$, upper index). 1 – alpine heaths; 2 – raised bogs; 3 – rich fens. The species occurring in only one column with frequency < 10 were excluded from the table, as well as the species of $\Phi < 0.20$.

complete linkage as the linkage method. 49 out of 79 relevés represent mature hummocks, the remainder are juvenescent hummocks or disintegrating structure. The data set of mature hummocks was divided into three clusters, which correspond with the most remarkable groups of turf hummock vegetation.

Cluster A

This group of relevés represents the ass. *Sphagnum capillifolium* – *Empetretum nigri* subass. *luzuletosum alpino pilosae* Bělohávková in Šibík *et al.* 2006. This is a two layered community occurring in the alpine level.

Cluster B

This cluster represents species poor community wide-spread in raised bogs, ass. *Vaccinium vitis-idaei* – *Sphagnum capillifolium*, subass. *eriphoretosum vaginati*. The sub-association is restricted to raised bog environment. Apart from co-dominated moss species *Sphagnum capillifolium* and *Polytrichum strictum* the moss layer is

characterised by many liverwort species.

Cluster C

This cluster represents two layered species rich community ass. *Vaccinio vitis-idaei* – *Sphagnetum capillifolii*, subass. *typicum*. The community is confined to rich fens.

Ordination

The detrended correspondence analysis (DCA) ordination diagram of 49 relevés shows the major differences in the direction of the first axis (length of gradient 4.887; eigenvalue 0.661) owing to the different moisture content available in the soil, correlated with temperature and

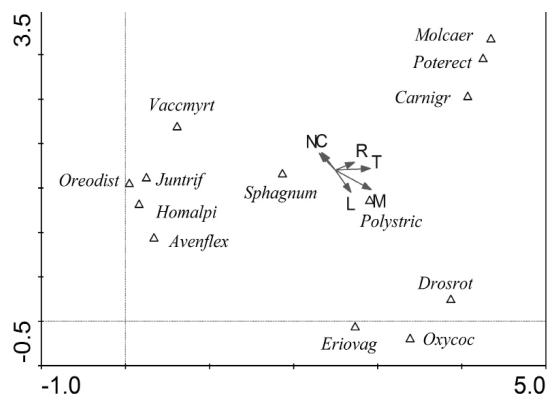


Fig. 1. Detrended correspondence analysis (DCA) ordination diagram of *Polytrichum* – *Sphagnum* hummocks data set. Ordination scores of the most important species (characteristic and differential species). Species list: Molcaer – *Molinia caerulea*, Poterect – *Potentilla erecta*, Carnigr – *Carex nigra*, Vaccmyrt – *Vaccinium myrtillus*, Oreodist – *Oreochloa disticha*, Juntrif – *Juncus trifidus*, Homalp – *Homogyne alpina*, Avenflex – *Avenella flexuosa*, Sphagnum – *Sphagnum capillifolium* incl. *S. rubellum*, Polystric – *Polytrichum strictum*, Drosrot – *Drosera rotundifolia*, Oxycoc – *Oxycoccus palustris* incl. *O. microcarpus*. L - light, T - temperature, C - continentality, M - moisture, R - acidity, N - nitrogen.

with pH level shifted to slightly acid. In the direction of the second axis (length of gradient 2.470; eigenvalue 0.358) the major gradient in species composition is associated with light (Fig. 1). Nutrient availability is negatively correlated with light, probably due to the development of broad-leaved herbs in nutrient-rich habitats, which decrease light availability near the soil surface.

The ordination of rich fen hummocks is positively correlated with moisture (1st axis) and with pH level changing to more neutral. This relevés are seen as diamonds on the right of Fig. 2. Raised bog hummocks are positively correlated with moisture and with pH level moved to acidic, relevant relevés are seen in the middle of Fig. 2 as triangles. The turf hummocks developed in the alpine level are positively correlated with reaction (1st axis) and tolerate relatively rich nutrient stocks. These relevés are seen on the left in Fig. 2 as squares.

Bog hummocks at the alpine level show higher concentrations of bivalent cations, sul-

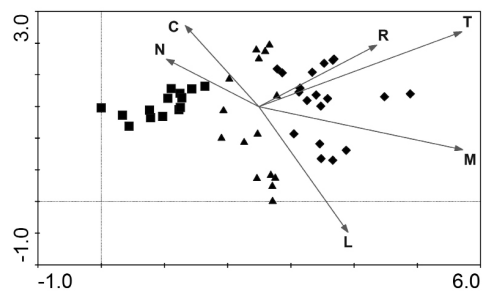


Fig. 2. Detrended correspondence analysis (DCA). Ordination of the hummocks data set. Squares – alpine level, triangles – raised bogs, diamonds – rich fens. L - light, T - temperature, C - continentality, M - moisture, R - acidity, N - nitrogen.

		pH	Cond.	Al ³⁺	NH ₄ ⁺	K ⁺	Na ⁺	Ca ²⁺	Mg ²⁺	NO ₃ ⁻	SO ₄ ²⁻	Cl ⁻
		2)	3)	mg.1000 ml ⁻¹								
Alpine level 1) mature hummock	Catotelm	6.03	155.20	9.65	0.23	2.05	5.74	22.4	8.51	4.59	16.30	0
Raised bog, mature hummock (Slepé pleso)	Catotelm	5.11	26.53	9.92	1.38	9.56	8.68	14.93	4.98	3.34	4.82	14.25
	Peat substratum	4.26	17.62	17.66	1.52	8.33	8.47	9.24	4.26	1.97	2.11	2.97
Rich fen, juvnescent stage (Bel- ské lúky)	Catotelm	7.05	297.33	26.84	19.58	31.03	12.85	25.38	7.79	22.06	18.45	0
	Peat substratum	7.81	354.73	41.62	21.14	35.81	11.12	43.37	9.94	36.01	43.27	0
Rich fen, mature hummock (Dobšinská řadová jaskyňa)	Catotelm	5.02	165.32	11.47	6.78	14.94	7.32	11.26	5.29	2.71	3.56	1.73
	Peat substratum	8.25	4385.37	32.38	23.94	47.13	12.71	95.82	51.98	41.63	50.22	4.14

1)peat substratum absent; 2) $\mu\text{S.cm}^2 / 20^\circ\text{C}$; 3) $\mu\text{g. 1000 ml}^{-1}$

Table 2. Catotelm and peat substrata chemistry.

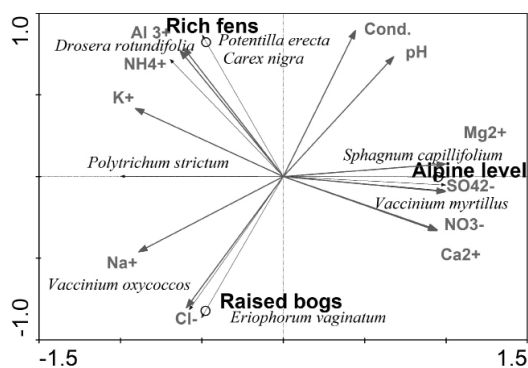


Fig. 3. Canonical correspondence analysis (CCA), trip-plot, ordination diagram of turf hummocks types, catotelm chemistry and selected plants. Mg^{2+} $p = 0.168$, $F = 44.824$.

phates and nitrates (Fig. 3). At this altitudes the hummocks are lower compared to hummocks in rich fens, the contact with the substratum is closer (Lamers *et al.* 1999) and mineral enrichment is possible. Contamination of hummocks surface layer by airborne salt particles is also possible.

Unexpectedly, the upper layer of the hummocks in rich fens is related to the most acidic environment (Table 2). Leaching of the hummock surface layers by rain waters makes this process more complicated. Laboratory experiments proved that mosses have the ability to adapt the environmental conditions to their requirements (Šmarda 1960). Nevertheless, the chemistry within the hummock catotelm is in every case different from that in the peat substratum (Table 2), they are raised above the influence of ground water and head towards more or less similarity in chemistry, independent of their origin.

Syntaxonomy and nomenclature

Class *Loiseleurio – Vaccinietea* Egger ex Schubert 1960
 Alliance *Loiseleurio – Vaccinion* Br.-Bl. in Br.-Bl. et Jenny 1926

Sphagno capillifolii – Empetretum nigri subass. *luzuletosum alpinopilosae* Bělohávková in Šibík *et al.* 2006

The community of alpine heaths described by Unar *et al.* (1985) was included in the subassociation as well as relevés covered turf hummocks sampled by Dúbravcová *et al.* (1976). This is a mosaic of bog turf hummocks and alpine heaths rich in *Sphagnum*. Alpine heaths are dominated by *Sphagnum girgensohnii* (or *Sphagnum russowii*) while turf hummocks are dominated by *Sphagnum capillifolium*, or by *Sphagnum rubellum* respectively. According to Šibík (2006), the *Sphagno capillifolii – Empetretum nigri* occupies the interface position between *Vaccinion myrtilli* and *Oxycocco – Empetrium hermaphroditi*. The occurrence of *Sphagnum magellanicum* in the floristical composition (Cykowska 2009) suggests possible inclusion of the community into the raised bogs. An extensive analytical material is needed to understand these communities, for the present, our relevés will be placed in the *Sphagno capillifolii – Empetretum nigri* subass. *luzuletosum alpinopilosae*.

The sub-association stands are optimally found at 1,700 – 1,900m a. s. l., dominating the north fac-

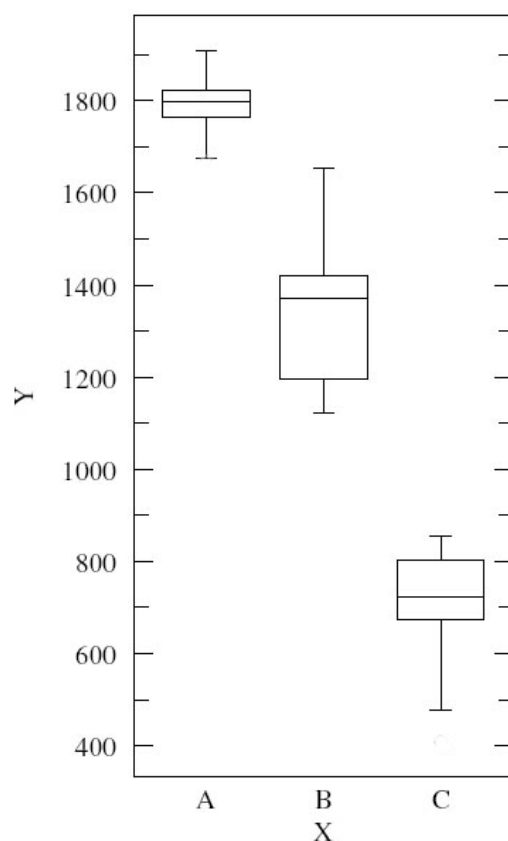


Fig. 4. Box and whisker plot of the altitude values. **X** - clusters: **A** – alpine heaths, **B** – raised bogs, **C** – rich fens; **Y** – altitude in m a.s.l.

ing slopes with an inclination between 20–40°. The community occurs in wet habitats, the source of moisture in springtime is a thick snow cover which persists until the end of May (Šibík *et al.* 2006), afterwards the community is nourished by precipitation. The habitats are protected from direct insolation and thereby from loss of water supply by evaporation from soil surface (Šibík *et al.* 2006). Physiognomy of the two-layer community is determined by co-dominance of *Sphagnum capillifolium* and *Polytrichum strictum* (Table 3) forming up to 70cm tall turf hummocks and by creeping chamaephytes. *Vaccinium vitis-idaea* and *Vaccinium myrtillus* occur constantly, *Avenella flexuosa*, *Juncus trifidus* and *Oreochloa disticha* are the most frequent hemicryptophytes. The size of these bogs fluctuates usually between 1 – 2.5m², occasionally up to 4m², but the stands may extend hundreds of square metres (Szwejkowski and Buczkowska 2000; Šibík *et al.* 2006). Despite a strong acidity of hummock upper layer (always near pH 3.1, Šibík *et al.* 2006; in Polish Tatra pH was from 4.03 to 4.42, Cykowska 2009), we could not observe any substitution of *Sphagnum capillifolium* by *Sphagnum rubellum*. *Cetraria islandica* is the most common lichen species, which becomes dominant when the hummocks start to disintegrate (see Table 7).

Class *Oxycocco – Sphagnetea* Br. - Bl. et R. Tx. ex Westhoff *et al.* 1946
 Alliance *Oxycocco – Empetrium hermaphroditi* Nordhagen 1936

Relevé No	0000000011111	12345678901234
Diagnostic species		
<i>Vaccinium vitis-idaea</i> (E ₁)	. 3 3 b a 3 b . a + 1 a + 1	
<i>Polytrichum strictum</i> (E ₀)	m 1 3 a 3 b 3 3 1 + + 3 3 a	
<i>Sphagnum capillifolium</i> (E ₀)	5 5 5 5 4 5 5 5 5 4 4 m 4 5	
Differential species		
<i>Vaccinium myrtillus</i>	4 4 b 4 3 4 3 b 4 3 + 3 3 4	
<i>Avenella flexuosa</i>	1 1 . 1 3 1 1 3 b 1 . 3 + 1	
<i>Juncus trifidus</i>	. 1 1 m . . a b 1 + + 1 1 +	
<i>Oreochloa disticha</i>	. . . + . + . + + + + + + +	
<i>Homogyne alpina</i>	. 1 . + + . + + . 1 1 1 +	
Other species		
<i>Vaccinium gaultherioides</i> + m . 3 a . . .	
<i>Gentiana punctata</i>	+ 1 . + . . .	
<i>Campanula alpina</i> 1 1 + 1 +	
<i>Ligusticum mutellina</i> + a . + + .	
<i>Agrostis rupestris</i> 1 1 + + .	
<i>Festuca supina</i> 1 + + . +	
<i>Luzula alpinopilosa</i> + + 1 + +	
<i>Calamagrostis villosa</i>	1 a +	
<i>Hieracium alpinum</i>	. + 1 + . . .	
<i>Pulsatilla scherfelii</i> + a	
<i>Huperzia selago</i> + r + . . .	
<i>Avenula versicolor</i> + +	
Bryophytes and lichens (E₀)		
<i>Pleurozium schreberi</i>	. + . . 1 + + 1 . .	
<i>Cetraria islandica</i> 1 1 b 1 1	
<i>Polytrichum alpinum</i>	. . + + + + . .	
<i>Sphagnum girgensohnii</i>	. . m 1	
<i>Cetraria cucullata</i> + . + +	
<i>Alectoria ochroleuca</i> + + +	
<i>Dicranum scoparium</i> + +	

Taxa occurring only in one relevé:

E₁: *Hieracium alpinum* 10: 1; *Doronicum stiriicum* 10: a; *Empetrum hermaphroditum* 11: +; *Leucanthemopsis alpina* 11: 1; *Salix kitaibeliana* 11: 1; *Carex sempervirens* 11: +; *Soldanella carpatica* 11: +; *Pedicularis verticillata* 11: +; *Carex atrata* 11: +; *Leontodon pseudotaraxaci* 11: +; *Ranunculus pseudomontanus* 11: +; *Primula minima* 11: +; *Polygonum bistorta* 13: +; *Nardus stricta* 14: +; E₀: *Calyptogeia neesiana* 4: +; *Barbilophozia lycopodioides* 10: +; *Lophozia sudetica* 12: +; *Hylocomium splendens* 12: +; *Cladonia rangiferina* 12: +; *Cladonia gracilis* 12: +.

Table 3. Turf hummock communities confined to alpine heaths, *Sphagno capillifolii* - *Empetretum nigri luzuleto-sum alpinopilosae*

Relevé locations:

1. The West Tatra Mts, Velká kopa, altitude 1,731 m a.s.l., area 1.0 x 1.0 m, total cover 100%, E₁ 60%, E₀ 100%, hummock height 40 cm, October 12, 2006, 49° 11.947' ; 19° 58.907' , accuracy 8 m.
2. The West Tatra Mts, Velká kopa, altitude 1,779 m a.s.l., area 1.5 x 1.5 m, total cover 100%, E₁ 60%, E₀ 100%, hummock height 30 cm, October 12, 2006, 49° 11.934' ; 19° 58.883' , accuracy 8 m.
3. The West Tatra Mts, Velká kopa, altitude 1,775 m a.s.l., area 1.0 x 1.0 m, total cover 100%, E₁ 100%, E₀ 80%, hummock height 40 cm, October 12, 2006, 49° 11.927' ; 19° 58.879' , accuracy 8 m.

4. The West Tatra Mts, Velká kopa, altitude 1,778 m a.s.l., area 1.5 x 1.5 m, total cover 100%, E₁ 60%, E₀ 100%, hummock height 20 cm, October 12, 2006, 49° 11.920' ; 19° 58.871' ,
5. The West Tatra Mts, Velká kopa, altitude 1,795 m a.s.l., area 1.5 x 0.7 m, total cover 100%, E₁ 80%, E₀ 100%, hummock height 50 cm, October 12, 2006, 49° 11.922' ; 19° 58.869' , accuracy 6 m.
6. The West Tatra Mts, Velká kopa, altitude 1,800 m a.s.l., area 1.0 x 1.0 m, total cover 100%, E₁ 70%, E₀ 100%, hummock height 40 cm, October 12, 2006, 49° 11.914' ; 19° 58.861' , accuracy 6 m.
7. The West Tatra Mts, Velká kopa, altitude 1,840 m a.s.l., area 2.0 x 0.8 m, total cover 100%, E₁ 50%, E₀ 100%, hummock height 60 cm, October 12, 2006, 49° 11.899' ; 19° 58.826' , accuracy 8 m.
8. The West Tatra Mts, Velká kopa, altitude 1,845 m a.s.l., area 1.5 x 0.8 m, total cover 100%, E₁ 70%, E₀ 100%, hummock height 30 cm, October 12, 2006, 49° 11.899' ; 19° 58.828' , accuracy 8 m.
9. The High Tatra Mts, Furkotská dolina Valley, altitude 1,908 m a.s.l., area 1.5 x 0.5 m, W aspect, inclination 40°, total cover 100%, E₁ 90%, E₀ 100%, hummock height 20 cm, October 14, 2008, 49° 09.054' ; 20° 01.966' , accuracy 8 m.
10. The West Tatra Mts, Bobrovecká dolina Valley, altitude 1,750 m a.s.l., area 12 m², N aspect, inclination 20°, cover E₁ 95%, E₀ 60%, 30. 8. 12974, leg. Dúbravcová *et al.* (1976).
11. The West Tatra Mts, Parichvost Valley, altitude 1,800 m a.s.l., area 50 m², WNW aspect, inclination 30°, cover E₁ 45%, E₀ 85%, 3. 9. 1975, leg. Dúbravcová *et al.* (1976).
12. The West Tatra Mts, Bobrovecká dolina Valley, altitude 1,670 m a.s.l., area 12 m², W aspect, inclination 15°, E₁ 80%, E₀ 100%, August 30, 1974, leg. Dúbravcová *et al.* (1976).
13. The West Tatra Mts, Jarnická dolina Valley, altitude 1,820 m a.s.l., area 20 m², N aspect, inclination 45°, E₁ 65%, E₀ 90%, September 14, 1974, leg. Dúbravcová *et al.* (1976).
14. The West Tatra Mts, Račková dolina Valley, altitude 1,700 m a.s.l., area 18 m², NW aspect, inclination 45°, E₁ 85%, E₀ 100%, August 12, 1975, leg. Dúbravcová *et al.* (1976)

Vaccinio vitis-idaei – *Sphagnetum capillifolii* Šoltés et Školek ass. nov. hoc loco

Typical physiognomy of a two-layer community is determined by turf hummocks co-dominated by *Sphagnum capillifolium* and *Polytrichum strictum* and often by creeping dwarf shrubs. In strongly acid habitats, *Sphagnum capillifolium* may be replaced by *Sphagnum rubellum*. The sizes of stands vary from roughly 0.5m² to several hundreds square meters. Deeper layer of thick cushions of bog mosses serve as an isolator. The association occupies raised bogs, rich or poor fens with little variance in floristic composition.

The communities described by Unar *et al.* (1985), Hadač (1956) and by Sillinger (1933) are not identical with the suggested association *Vaccinio vitis-idaei* – *Sphagnetum capillifolii*. These zonal subalpine communities are rich in different *Sphagnum* species forming a thick layer of acid humus and do not create turf hummocks codominated by *Sphagnum capillifolium* and *Polytrichum strictum* as a result of decline in decomposition.

Non: *Sphagno* – *Empetretum her-maphroditi* Unar in Unar *et al.* 1985, *Sphagneto* – *Caricetum pauciflorae* Hadač 1956, *Sphagneto* – *Trichophoretum alpini* Hadač 1956.

Nomenclatural type: Table 4, rel. 4, holotypus
Diagnostic taxa: *Vaccinium vitis-idaea* (char.), *Sphagnum capillifolium* (dom.), *Polytrichum strictum* (dom.)

Relevé No	000000001111111111 1234567890123456789
Diagnostic species	
<i>Vaccinium vitis-idaea</i> (E ₁)	..ab..34332+bb3....
<i>Polytrichum strictum</i> (E ₀)	433434555355554333
<i>Sphagnum capillifolium</i> (E ₀)	b3m5554..54.14.1555
<i>Sphagnum rubellum</i> (E ₀)	..4....43..m4.45...
Differential species	
<i>Potentilla erecta</i>	ab1+111a++..11a13m3m
<i>Drosera rotundifolia</i>	..m+1.....am1mma+
<i>Carex nigra</i>	+..+1m+1...+..b1a11...
<i>Molinia caerulea</i>	3mmm..+mm++....+3aa
Other species	
<i>Oxycoccus palustris</i>	..1+a m.....
<i>Equisetum palustre</i>	..1a1bm.m.+.....1..
<i>Succisa pratensis</i>	..m.1..ab1m+..+..b...
<i>Pinus sylvestris</i>	1..++..1m+....+..r
<i>Frangula alnus</i>	b.a.ba.....+...m11
<i>Betula pendula</i>	1m.....++..+..+..
<i>Calluna vulgaris</i>	..m.+.....
<i>Carex paniculata</i>+1mm..1..b...
<i>Galium uliginosum</i>	11.....+.....1..
<i>Menyanthes trifoliata</i>	..a111a.....
<i>Picea abies</i>	..a..+..+..11.+....
<i>Cirsium palustre</i>++1+..+...+1..
<i>Galium palustre</i>	1+....m..+.....
<i>Lathyrus pratensis</i>+..+..+..
<i>Parnassia palustris</i>	m+.....+.....
<i>Briza media</i>	1.....+.....
<i>Lysimachia vulgaris</i>	..1a.+.....+.....
<i>Epipactis palustris</i>	..+..11.....1..
<i>Filipendula ulmaria</i>+++.....
<i>Pyrola rotundifolia</i>+.....m
<i>Salix cinerea</i>+.....1....
<i>Festuca rubra</i>+.....+..
<i>Juncus articulatus</i>	11.....
<i>Ligularia sibirica</i>++1.....
<i>Angelica sylvestris</i>+++.....
<i>Carex panicea</i>m.m1....
<i>Carex flava</i>	+b.....
<i>Crepis paludosa</i>+.....
<i>Vaccinium myrtillus</i>1b
Bryophytes (E₀)	
<i>Tomentypnum nitens</i>	bb...1.....
<i>Aulacomnium palustre</i>	ma..+.....
<i>Sphagnum fallax</i>11.+.....

Taxa occurring only in one relevé:

E₂: *Salix cinerea* 15: b;

E₁: *Valeriana simplicifolia* 2: 1; *Primula farinosa* 2: 1; *Eriophorum angustifolium* 3: 1; *Epilobium palustre* 4: 1; *Gymnadenia conopsea* 5: +; *Solidago virgaurea* 7: +; *Salix pentandra* 8: 1; *Chaerophyllum aromaticum* 8: +; *Geum rivale* 8: +; *Maianthemum bifolium* 8: +; *Swertia perennis* 10: r; *Corylus avellana* 11: +; *Sorbus aucuparia* 12: r; *Veronica chamaedrys* 15: +; *Cruciata glabra* 17: +.

E₀: *Polytrichum commune* 5: +; *Sphagnum palustre* 17:

Table 4. Turf hummock communities confined to rich fens, *Vaccinio vitis-idaei* – *Sphagnetum capillifolii* typicum.

Relevé locations:

1. Popradská kotlina basin, Belské lúky fen, altitude 673 m a.s.l., area 0.5 x 0.5 m, total cover 100%, E₁ 60%, E₀ 100%, hummock height 20 cm, September 24, 2007, 49° 12.873' ; 20° 23.602' , accuracy 8 m.
2. Popradská kotlina basin, Belské lúky fen, altitude 674 m a.s.l., area 0.5 x 0.5 m, total cover 100%, E₁ 50%, E₀ 100%,

hummock height 20 cm, September 24, 2007, 49° 12.854' ; 20° 23.554' , accuracy 8 m.

3. Liptovská kotlina basin, Pribylina, Lazy, altitude 790 m a.s.l., area 1.5 x 1.5 m, E aspect, inclination 2° , total cover 100%, E₁ 50%, E₀ 95%, hummock height 60 cm, July 30, 2009, 49° 06.716' ; 19° 48.760' , accuracy 6 m.
4. Liptovská kotlina basin, Pribylina, Lazy, altitude 790 m a.s.l., area 1.0 x 0.7 m, E aspect, inclination 2° , total cover 100%, E₁ 40%, E₀ 100%, hummock height 60 cm, July 30, 2009, 49° 06.714' ; 19° 48.762' , accuracy 6 m.
5. Liptovská kotlina basin, Pribylina, Lazy, altitude 790 m a.s.l., area 0.5 x 0.5 m, E aspect, inclination 2° , total cover 100%, E₁ 60%, E₀ 100%, hummock height 25 cm, July 30, 2009, 49° 06.715' ; 19° 48.756' , accuracy 6 m.
6. Liptovská kotlina basin, Pribylina, Lazy, altitude 791 m a.s.l., area 1.0 x 0.5 m, E aspect, inclination 2° , total cover 100%, E₁ 60%, E₀ 100%, hummock height 30 cm, July 30, 2009, 49° 06.718' ; 19° 48.738' , accuracy 11 m.
7. Slovenský raj Paradise, fen near railway station Dobšinská Ladová Jaskyňa, altitude 851 m a.s.l., area 4.0 x 3.0 m, plain, total cover 100%, E₁ 60%, E₀ 100%, hummock height 50 cm, August 9, 2009, 48° 52.514' ; 20° 17.742' , accuracy 6 m.
8. Slovenský raj Paradise, fen near railway station Dobšinská Ladová Jaskyňa, altitude 851 m a.s.l., area 5.0 x 5.0 m, plain, total cover 100%, E₁ 80%, E₀ 100%, hummock height 50 cm, August 9, 2009, 48° 52.517' ; 20° 17.737' , accuracy 6 m.
9. Slovenský raj Paradise, fen near railway station Dobšinská Ladová Jaskyňa, altitude 851 m a.s.l., area 3.0 x 2.0 m, plain, total cover 100%, E₁ 40%, E₀ 100%, hummock height 40 cm, August 9, 2009, 48° 52.518' ; 20° 17.737' , accuracy 8 m.
10. Slovenský raj Paradise, fen near railway station Dobšinská Ladová Jaskyňa, altitude 851 m a.s.l., area 3.0 x 2.0 m, plain, total cover 100%, E₁ 40%, E₀ 100%, hummock height 40 cm, August 9, 2009, 48° 52.514' ; 20° 17.739' , accuracy 8 m.
11. Slovenský raj Paradise, fen near railway station Dobšinská Ladová Jaskyňa, altitude 851 m a.s.l., area 1.0 x 0.7 m, plain, total cover 100%, E₁ 20%, E₀ 100%, hummock height 30 cm, August 9, 2009, 48° 52.507' ; 20° 17.727' , accuracy 8 m.
12. Muránska planina, land register Zlatno, altitude 723 m a.s.l., area 3.0 x 3.0 m, plain, total cover 100%, E₁ 30%, E₀ 100%, hummock height 30 cm, August 10, 2009, 48° 49.108' ; 20° 03.779' , accuracy 7 m.
13. Muránska planina, land register Zlatno, altitude 723 m a.s.l., area 2.0 x 1.0 m, plain, total cover 100%, E₁ 30%, E₀ 100%, hummock height 70 cm, August 10, 2009, 48° 49.117' ; 20° 03.769' , accuracy 8 m.
14. Muránska planina, land register Zlatno, altitude 723 m a.s.l., area 1.5 x 1.0 m, plain, total cover 100%, E₁ 30%, E₀ 100%, hummock height 40 cm, August 10, 2009, 48° 49.112' ; 20° 03.772' , accuracy 7 m.
15. Muránska planina, land register Zlatno, altitude 723 m a.s.l., area 2.0 x 4.0 m, plain, total cover 100%, E₁ 50%, E₀ 100%, hummock height 60 cm, August 10, 2009, 48° 49.110' ; 20° 03.769' , accuracy 9 m.
16. Muránska planina, land register Zlatno, altitude 723 m a.s.l., area 1.0 x 1.0 m, plain, total cover 100%, E₁ 80%, E₀ 100%, hummock height 40 cm, August 10, 2009, 48° 49.113' ; 20° 03.777' , accuracy 10 m.
17. Veľká Fatra Mts, Rojkovské rašelinisko fen, 409 m a.s.l., area 1.5 x 0.7 m, plain, total cover 100%, E₁ 80%, E₀ 100%, hummock height 20 cm, August 12, 2009, 49° 08.932' ; 19° 09.293' , accuracy 7 m.
18. Veľká Fatra Mts, Rojkovské rašelinisko fen, 409 m a.s.l., area 1.5 x 1.5 m, plain, total cover 100%, E₁ 5%, E₀ 100%, hummock height 30 cm, August 12, 2009, 49° 08.927' ; 19° 09.281' , accuracy 7 m.
19. Veľká Fatra Mts, Rojkovské rašelinisko fen, 409 m a.s.l., area 1.0 x 0.7 m, plain, total cover 100%, E₁ 30%, E₀ 100%, hummock height 20 cm, August 12, 2009, 49° 08.930' ; 19° 09.261' , accuracy 12 m.

Vaccinio vitis-idaei – *Sphagnetum capillifolii* typicum Šoltés et Školek subass. nov. hoc loco

This closed community is characterised by the participation of chamaephytes where *Vaccinium vitis-idaea* sometimes dominates amongst the chamaephytes. *Sphagnum capillifolium* is sometimes partly or wholly replaced by *Sphagnum rubellum*. In the early stages of development of the sub-association, ground water is essential, but later nourishment is provided by precipitation. These stands are strictly confined to minerotrophic mires at altitudes of 409 – 855 m a. s. l. Sometimes numbers of such hummocks are sited parallel to one another and inter-hummock areas are also covered by *Sphagnum* – *Polytrichum* growth, so the extent of these communities fluctuate between (0.5) 1 m² to hundreds of square metres, e. g. the mire near Dobšinská Ladová Jaskyňa. The hummocks are often tall, reaching up to 70 cm, ensuring perfect separation from the basic mire substratum. In marginal areas where this layer is not so thick and plant roots could maintain contact with the mineral rich peat substratum, typical fen plants are found. Apart from differential taxa, more hemicyptophytes like *Equisetum palustre*, *Succisa pratensis*, *Cirsium palustre* are very frequently present.

Nomenclatural type: Identical with the type of the association.

Differential taxa: *Potentilla erecta*, *Drosera rotundifolia*, *Molinia caerulea*, *Carex nigra*.

Vaccinio vitis-idaei – *Sphagnetum capillifolii* eriophoretosum vaginati Šoltés et Školek subass. nov. hoc loco

The sub-association requires ground water in the early stages of its development, later deriving moisture from precipitation. The phytocoenoses are exclusively associated with raised bog habitats at altitudes between 1,121 – 1,653 m a. s. l. *Physiognomy* of the two-layer, closed community is conditioned by the codominant species *Sphagnum capillifolium* and *Polytrichum strictum*, creating hummocks, up to 60 cm. When hummocks get older, *Sphagnum capillifolium* is partly replaced by *Sphagnum rubellum*. In regards to chamaephytes, only *Oxycoccus palustris* (incl. *O. microcarpus*) reaches significant presence. Hemicyptophytes occur at low numbers, *Carex rostrata* being an exception. The size of these miniature bogs varies between 0.3 – 2.2 m².

Nomenclatural type: Table 5, rel. 11, holotypus

Differential taxa: *Eriophorum vaginatum*, *Oxycoccus palustris* (incl. *O. microcarpus*)

Turf hummocks life cycle

The ombrotrophic mire is ultimately limited in the depth of its peat development by microbial respiration within the catotelm. As the catotelm extends with peat accumulation, the total respiratory activity of the profile will equilibrate with primary productivity and peat formation slowing down to an eventual standstill (Moore 1995).

Relevé No	00000000111111 1234567890123456
Diagnostic species	
<i>Vaccinium vitis-idaea</i> (E ₁) 4 b 3 3 3.
<i>Polytrichum strictum</i> (E ₀)	44454354b3434b33
<i>Sphagnum capillifolium</i> (E ₀)	a33a31m454555555
<i>Sphagnum rubellum</i> (E ₀)	b..... 3.....
Differential species	
<i>Eriophorum vaginatum</i>	1m1aababbb3341a4
<i>Oxycoccus palustris</i> +. mba2bm.
<i>Oxycoccus microcarpus</i>	1 a b a + a.....
Other species	
<i>Vaccinium myrtillus</i> a..... 3 b
<i>Drosera rotundifolia</i>	.. + 1 + 1.....
<i>Calluna vulgaris</i> 1 m b....
<i>Pinus mugo</i> ++ abb+..
<i>Carex rostrata</i>	.. m m 2 a... 1.....
<i>Carex limosa</i>	+ 1 r 1.....
<i>Scheuchzeria palustris</i>	. r . . + 1.....
<i>Gentiana punctata</i> 1 . . +.....
<i>Carex pauciflora</i> +..... 1
Bryophytes (E ₀)	
<i>Sphagnum magellanicum</i>	m..... m. m. 1. +. 1
<i>Cephalozia lunulifolia</i>	. + 1. + +.....
<i>Sphagnum fallax</i>	.. + +. +..... 1....
<i>Gymnocolea inflata</i>	... + 1 1.....
<i>Drepanocladus fluitans</i>	. 1 b.....
Taxa occurring in only one relevé:	
E ₁ : <i>Avenella flexuosa</i> 2: +; <i>Homogyne alpina</i> 7: 1; <i>Vaccinium uliginosum</i> 1: 1; <i>Carex canescens</i> 3: 1; <i>Betula* carpatica</i> 14: +;	
E ₀ : <i>Myliia anomala</i> 5: +.	

Table 5. Turf hummock communities confined to raised bogs, *Vaccinio vitis-idaei* - *Sphagnetum capillifolii* eriophoretosum vaginati.

Relevé locations:

1. The High Tatra Mts, Slepé pleso raised bog, altitude 1,370 m a.s.l., area 1.0 x 1.0 m, total cover 100%, E₁ 10%, E₀ 100%, hummock height 20 cm, September 13, 2007, 49° 07.515' ; 20° 03.187' , accuracy 5 m.
2. The High Tatra Mts, Slepé pleso raised bog, altitude 1,370 m a.s.l., area 1.5 x 2.0 m, total cover 100%, E₁ 25%, E₀ 100%, hummock height 20 cm, September 13, 2007, 49° 07.530' ; 20° 03.192' , accuracy 5 m.
3. The High Tatra Mts, Slepé pleso raised bog, altitude 1,370 m a.s.l., area 1.0 x 1.0 m, total cover 100%, E₁ 30%, E₀ 100%, hummock height 20 cm, September 13, 2007, 49° 07.521' ; 20° 03.238' , accuracy 5 m.
4. The High Tatra Mts, Slepé pleso raised bog, altitude 1,370 m a.s.l., area 1.0 x 1.5 m, total cover 100%, E₁ 25%, E₀ 100%, hummock height 15 cm, September 13, 2007, 49° 07.513' ; 20° 03.226' , accuracy 5 m.
5. The High Tatra Mts, Slepé pleso raised bog, altitude 1,370 m a.s.l., area 0.8 x 1.5 m, total cover 100%, E₁ 20%, E₀ 100%, hummock height 10 cm, September 13, 2007, 49° 07.513' ; 20° 03.226' , accuracy 6 m.
6. The High Tatra Mts, Slepé pleso raised bog, altitude 1,370 m a.s.l., area 1.5 x 1.5 m, total cover 100%, E₁ 30%, E₀ 100%, hummock height 30 cm, September 13, 2007, 49° 07.511' ; 20° 03.233' , accuracy 6 m.
7. The High Tatra Mts, Žabia Bielovodská dolina Valley, raised bog, altitude 1,653 m a.s.l., area 0.5 x 0.5 m, total cover 100%, E₁ 10%, E₀ 100%, hummock height 15 cm, July 15, 2009, 49° 12.038' ; 20° 05.750' , accuracy 5 m.
8. The High Tatra Mts, Kolová dolina Valley, raised bog, altitude 1,565 m a.s.l., area 0.5 x 0.7 m, total cover 100%, E₁ 30%, E₀ 100%, hummock height 30 cm, July 21, 2009, 49° 13.290' ; 20° 11.496' , accuracy 6 m.
9. The High Tatra Mts, Kolová dolina Valley, raised bog,

- altitude 1,565 m a.s.l., area 0.5 x 0.7 m, total cover 100%, E₁ 40%, E₀ 100%, hummock height 20 cm, July 21, 2009, 49° 13.302' ; 20° 11.465' , accuracy 6 m.
10. The High Tatra Mts, Kolová dolina Valley, raised bog, altitude 1,565 m a.s.l., area 0.5 x 0.7 m, total cover 100%, E₁ 40%, E₀ 100%, hummock height 15 cm, July 21, 2009, 49° 13.288' ; 20° 11.509' , accuracy 5 m.
11. The High Tatra Mts, Christlová raised bog, altitude 1,121 m a.s.l., area 2.0 x 1.0 m, plain, total cover 100%, E₁ 80%, E₀ 100%, hummock height 30 cm, August 17, 2009, 49° 09.775' ; 20° 14.469' , accuracy 5 m.
12. The High Tatra Mts, Christlová raised bog, altitude 1,121 m a.s.l., area 1.5 x 1.0 m, plain, total cover 100%, E₁ 80%, E₀ 100%, hummock height 30 cm, August 17, 2009, 49° 09.777' ; 20° 14.482' , accuracy 8 m.
13. The High Tatra Mts, Christlová raised bog, altitude 1,121 m a.s.l., area 1.5 x 0.7 m, plain, total cover 100%, E₁ 90%, E₀ 100%, hummock height 35 cm, August 17, 2009, 49° 09.776' ; 20° 14.502' , accuracy 7 m.
14. The High Tatra Mts, Christlová raised bog, altitude 1,121 m a.s.l., area 1.0 x 1.0 m, plain, total cover 100%, E₁ 40%, E₀ 100%, hummock height 35 cm, August 17, 2009, 49° 09.786' ; 20° 14.481' , accuracy 7 m.
15. The High Tatra Mts, Christlová raised bog, altitude 1,121 m a.s.l., area 2.0 x 2.0 m, plain, total cover 100%, E₁ 70%, E₀ 100%, hummock height 60 cm, August 17, 2009, 49° 09.787' ; 20° 14.496' , accuracy 8 m.
16. The High Tatra Mts, Rakytové plesko raised bog, altitude 1,435 m a.s.l., area 0.5 x 0.7 m, plain, total cover 100%, E₁ 70%, E₀ 100%, hummock height 25 cm, September 1, 2009, 49° 07.889' ; 20° 02.119' , accuracy 7 m.

Relatively well-structured turf hummocks developed in as little as 20 years (Gill 1973), their destruction by desiccation and erosion taking around 60 years (Raup 1966). A big hummock recoved by Cykowska (2009) in the Polish Tatras and studied with metod of carbon C¹⁴ was determined as about 60 years old (145.87 ± 0.44 pMC; Poz-22868). The life cycle of hummocks described by Szweykowski and Buczkowska (2000), show that after reaching a height of about 50 cm they begin to disintegrate although hummocks sometimes begin to grow again on the same, freshly denuded surface.

Juvenescent phase

Initial stages vary in different habitats. In rich fens or in alpine heaths, the origin of hummock usually start with a local *Sphagnum* sp. colonisation. When the hummock is getting older and higher and the hummock is isolated enough from the substratum to maintain sufficient acidity, *Sphagnum capillifolium* is being expanded and *Polytrichum strictum* is being incorporated.

Hummocks developing in rich fens contain species typical of a rich fen flora, but these never occur in mature hummocks, e.g. *Primula farinosa*, *Juncus bulbosus*, *Carex flacca*, *Blysmus compressus* and many others, including bryophytes like *Tomentypnum nitens*, *Calliergonella cuspidata*, *Climacium dendroides*, *Sphagnum teres* and others. Examples of juvenescent hummocks developing in rich fen habitats are presented in Table 6.

The juvenescent hummocks in alpine heaths are low and poor in number of species, but chamaephytes are present.

Example: The High Tatra Mts, Furkotská dolina valley, 2,075 m a. s. l., area 0.5 x 0.5 m, SW aspect, inclination 20° , total cover 100%, E₁ 40%, E₀ 100%, the hummock height 5 cm, 14.

Relevé No	123456
E ₁	
<i>Potentilla erecta</i>	m.++++
<i>Molinia caerulea</i>	m....4
<i>Carex nigra</i>	+a....
<i>Equisetum palustre</i>	1.b3b1
<i>Succisa pratensis</i>	+...+
<i>Carex paniculata</i>	..3.3.
<i>Carex rostrata</i>	1b.+..
<i>Galium uliginosum</i>	m..+m
<i>Menyanthes trifoliata</i>	11....
<i>Galium palustre</i>	+...+
<i>Lathyrus pratensis</i>	..+..
<i>Parnassia palustris</i>	1...+
<i>Briza media</i>	1...+
<i>Valeriana simplicifolia</i>	..1+1+
<i>Salix cinerea</i>	1...1
<i>Festuca rubra</i>	...+.
Bryophytes (E ₀)	
<i>Sphagnum capillifolium</i>	55.555
<i>Polytrichum strictum</i>	1...1
<i>Sphagnum rubellum</i>	..5a..
<i>Aulacomnium palustre</i>	m..m.a
<i>Tomentypnum nitens</i>	m.a...

Other species:

E₂: *Salix pentandra* 2: 1; *Salix cinerea* 2: 4; *Salix silesiaca* 2: 1;
E₁: *Frangula alnus* 1: 3; *Sanguisorba minor* 1: a; *Juncus bulbosus* 1: +; *Carex flacca* 1: +; *Viola palustris* 1: 1; *Pyrola rotundifolia* 1: 1; *Juncus articulatus* 1: +; *Gymnadenia conopsea* 1: +; *Blysmus compressus* 2: 1; *Myosotis scorpioides* 2: +; *Eriophorum latifolium* 2: +; *Lycopus europaeus* 2: +; *Drosera rotundifolia* 6: m; *Betula pendula* 6: b; *Lysimachia vulgaris* 6: 1; *Epipactis palustris* 6: 1; *Primula farinosa* 6: 1; *Luzula campestris* 6: r;
E₀: *Sphagnum teres* 2: 4; *Calliergonella cuspidata* 2: 1; *Sphagnum squarrosum* 2: 1; *Drepanocladus cossonii* 2: +; *Plagiomnium affine* 2: 1.

Table 6. Juvenescent hummocks developing in rich fens.

Relevé locations:

1. Popradská kotlina basin, Belské lúky fen, altitude 675 m a.s.l., area 1.0 x 0.5 m, total cover 100%, E₁ 60%, E₀ 100%, hummock height 20 cm, September 24, 2007, 49° 12.840' ; 20° 23.559' , accuracy 6 m.
2. Spišská Magura, Veľké Osturnianske jazero fen, altitude 818 m a.s.l., area 1.5 x 1.5 m, total cover 100%, E₂ 80%, E₁ 50%, E₀ 100%, hummock height 20 cm, September 10, 2008, 49° 20.457' ; 20° 13.241' , accuracy 7 m.
3. Muránska planina, Havraník, fen, altitude 757 m a.s.l., area 0.5 x 1.0 m, total cover 100%, E₁ 70%, E₀ 100%, hummock height 25 cm, July 23, 2009, 48° 48.979' ; 20° 03.606' , accuracy 7 m.
4. Muránska planina, Havraník, fen, altitude 757 m a.s.l., area 0.5 x 1.0 m, total cover 100%, E₁ 50%, E₀ 100%, hummock height 35 cm, July 23, 2009, 48° 48.974' ; 20° 03.613' , accuracy 7 m.
5. Muránska planina, Havraník, fen, altitude 757 m a.s.l., area 0.7 x 1.0 m, total cover 100%, E₁ 70%, E₀ 100%, hummock height 30 cm, July 23, 2009, 48° 48.977' ; 20° 03.608' , accuracy 7 m.
6. Veľká Fatra Mts, Rojkovské rašelinisko fen, 409 m a.s.l., area 1.5 x 0.5 m, plain, total cover 100%, E₁ 90%, E₀ 100%, hummock height 15 cm, August 12, 2009, 49° 08.934' ; 19° 09.292' , accuracy 7 m.

10. 2008: *Oreochloa disticha* 3, *Agrostis rupestris* 2m, *Salix herbacea* 1, *Sphagnum capillifolium* 5.

In juvenescent hummocks developing in acid

raised bog, *Sphagnum capillifolium*, *Polytrichum strictum* and chamaephytes are associated already in early successional pathways, examples:

Example 1: The High Tatra Mts, raised bog Christlová, 1,121 m a. s. l. area 0.3 x 0.3 m, total cover 100%, E₁ 95%, E₀ 100%, the hummock height 10 cm, 17. 8. 2009, 49° 09.776' , 20° 14.481' : *Eriophorum vaginatum* 5, *Calluna vulgaris* 3, *Vaccinium vitis-idaea* 1, *Vaccinium oxycoccos* 2m, *Sphagnum capillifolium* 5, *Polytrichum strictum* 1.

Example 2: The High Tatra Mts, raised bog Christlová, 1,121 m a. s. l., the very incipient hummock of area 25 cm in diameter, total cover 100%, E₁ 20%, E₀ 100%, the hummock height 5 cm, 17. 8. 2009, 49° 09.784' , 20° 14.505' : *Vaccinium vitis-idaea* 2b, *Eriophorum vaginatum* 2a, *Sphagnum capillifolium* 5, *Polytrichum strictum* 4.

Unlike mature rich fen hummocks, in which shrubs are important components, their juvenescent counterparts have few chamaephytic associates (Table 6).

Disintegrating phase

A notable feature of the degrading hummocks in alpine heaths is the reduction of their *Sphagnum* and *Polytrichum* abundancy and expansion of the

Relevé No	12345678
<i>Vaccinium myrtillus</i>	4433 . a b3
<i>Juncus trifidus</i>	m+541 mm.
<i>Vaccinium vitis-idaea</i>	+ . 3 b a . . +
<i>Avenella flexuosa</i>	+ . . + . + + 3
<i>Oreochloa disticha</i>	+ . 1 + . + . +
<i>Vaccinium gaultherioides</i>	. 4 . . 5 3 3 .
<i>Hieracium alpicola</i>	+ . . . + . + .
<i>Empetrum hermaphroditum</i>	4 5 . .
Bryophytes (E ₀)	
<i>Cetraria islandica</i>	55555353
<i>Polytrichum alpinum</i>	+ . . + + . + .
<i>Polytrichum strictum</i>	. m + . . + . .
<i>Pleurozium schreberi</i>	. + 1 1 a . . .

Other species:

E₀: *Lophozia sudetica* 5: +; *Lophozia longiflora* 7: +; *Anastrophyllum minutum* 7: +.

Table 7. Disintegrated hummocks in alpine heaths.

Relevé locations

1. The West Tatra Mts, The Western Tatra Mts., altitude 1,761 m a.s.l., area 1.0 x 1.0 m, total cover 100%, E₁ 100%, E₀ 80%, hummock height 30 cm, October 12, 2006, 49° 11.940' ; 19° 58.888' , accuracy 6 m.
2. The West Tatra Mts, The Western Tatra Mts., Veľká kopa, altitude 1,763 m a.s.l., area 1.0 x 1.0 m, total cover 100%, E₁ 90%, E₀ 100%, hummock height 30 cm, October 12, 2006, 49° 11.940' ; 19° 58.888' , accuracy 6 m.
3. The West Tatra Mts, The Western Tatra Mts., Veľká kopa, altitude 1,775 m, area 1.0 x 1.0 m, total cover 100%, E₁ 100%, E₀ 90%, hummock height 30 cm, October 12, 2006, 49° 11.930' ; 19° 58.878' , accuracy 6 m.
4. The West Tatra Mts, The Western Tatra Mts., Veľká kopa, altitude 1,800 m a.s.l., area 1.5 x 0.8 m, total cover 100%, E₁ 100%, E₀ 100%, hummock height 30 cm, October 12, 2006, 49° 11.907' ; 19° 58.854' , accuracy 6 m.
5. The West Tatra Mts, The Western Tatra Mts., Veľká kopa, altitude 1,810 m a.s.l., area 1.5 x 0.8 m, total cover 100%, E₁ 80%, E₀ 100%, hummock height 30 cm, October 12, 2006, 49° 11.912' ; 19° 58.855' , accuracy 6 m.
6. The West Tatra Mts, The Western Tatra Mts., Veľká

kopa, altitude 1,815 m a.s.l., area 1.5 x 1.0 m, total cover 100%, E₁ 100%, E₀ 50%, hummock height 40 cm, October 12, 2006, 49° 11.900' ; 19° 58.836' , accuracy 6 m.

7. The West Tatra Mts, The Western Tatra Mts., Veľká kopa, altitude 1,825 m a.s.l., area 1.5 x 0.8 m, total cover 100%, E₁ 50%, E₀ 100%, hummock height 30 cm, October 12, 2006, 49° 11.901' ; 19° 58.887' , accuracy 6 m.

8. The West Tatra Mts, The Western Tatra Mts., Veľká kopa, altitude 1,854 m a.s.l., area 1.5 x 0.8 m, total cover 100%, E₁ 50%, E₀ 100%, hummock height 50 cm, October 12, 2006, 49° 11.895' ; 19° 58.825' , accuracy 6 m.

lichen *Cetraria islandica* (Table 7). More sensitive *Sphagnum capillifolium* rapidly disappears while *Polytrichum strictum* survives longer. Disintegrating hummocks are often dominated by *Empetrum hermaphroditum*.

While dessicated hummocks in alpine level are dominated by lichen *Cetraria islandica*, degraded structures in rich fens are covered by lichen *Cladonia coccifera* (cf. Fenton and Smith 1982).

In the case of very advanced dessication, the hummocks obtain an earth core, and such structures are dominated by *Thymus pulegioides* and by the moss *Pleurozium schreberi*.

Example: Muránska planina, dessicated hummock, altitude 723 m a. s. l., area 0.7 x 0.7 m, total cover 100%, E₁ 100%, E₀ 50%, hummock height 30 cm, August 10. 2009, 48° 49.123' , 20° 03.857' : *Thymus pulegioides* 4, *Leontodon hispidus* 2a, *Galium schultesii* 2a, *Lathyrus pratensis* 2a, *Deschampsia caespitosa* 2a, *Potentilla erecta* 2m, *Trifolium montanum* 1, *Anthoxanthum odoratum* 1, *Briza media* 1, *Lotus corniculatus* +, *Festuca ovina* +, *Achillea millefolium* +, *Ranunculus acris* +, *Pleurozium schreberi* 4.

Hummocks undergoing disintegration from

Relevé No	12345678
<i>Calluna vulgaris</i>	55455333
<i>Vaccinium vitis-idaea</i>	...1.323
<i>Potentilla erecta</i>	1.111...
<i>Eriophorum vaginatum</i>+24
<i>Molinia caerulea</i>	12.2....
<i>Equisetum palustre</i>	1.2+....
<i>Vaccinium myrtillus</i>	.2.3....
<i>Carex nigra</i>	+2.....
<i>Nardus stricta</i>	1...1...
<i>Pinus mugo</i>3.2
<i>Carex panicea</i>	1..+....
<i>Cruciata glabra</i>	+...+...
Bryophytes (E ₀)	
<i>Pleurozium schreberi</i>	.55.5535
<i>Polytrichum strictum</i>	1.11..++
<i>Sphagnum capillifolium</i>	2..3.+21

Other species:

E₁: *Rumex acetosa* 1: 1; *Vicia cracca* 1: +; *Hieracium murorum* 1: +; *Agrostis stolonifera* 1: +; *Anthoxanthum odoratum* 1: +; *Lathyrus pratensis* 1: +; *Briza media* 1: +; *Angelica sylvestris* 1: +; *Vaccinium oxycoccos* 3: 1; *Ranunculus acris* 3: 1; *Fragula alnus* 3: 2; *Menyanthes trifoliata* 3: 2; *Epipactis palustris* 3: 2; *Drosera rotundifolia* 4: +; *Arrhenatherum elatius* 5: 1; *Centaurea jacea* 5: +; *Juniperus communis* 5: 2; *Picea abies* 6: r; E₀: *Aulacomnium palustre* 1: +; *Hylocomium splendens* 5: +; *Polytrichum commune* 6: +.

Table 8. Disintegrated hummocks dominated by *Calluna vulgaris*. Relevés 1-5 are taken in rich fens, relevés 6-8 are taken in raised bogs.

Relevé locations:

1. Liptovská kotlina Basin, Pribylina, Lazy, altitude 799 m a.s.l., area 1.0 x 1.0 m, E aspect, inclination 2°, total cover 100%, E₁ 100%, E₀ 20%, hummock height 25 cm, August 27, 2009, 49° 06.715' ; 19° 48.741' , accuracy 12 m.
2. Liptovská kotlina Basin, Pribylina, Lazy, altitude 792 m a.s.l., area 0.5 x 0.5 m, E aspect, inclination 2° , total cover 100%, E₁ 95%, E₀ 90%, hummock height 30 cm, August 27, 2009, 49° 06.695' ; 19° 48.786' , accuracy 5 m.
3. Liptovská kotlina Basin, Pribylina, Lazy, altitude 796 m a.s.l., area 0.5 x 0.5 m, E aspect, inclination 2° , total cover 90%, E₁ 60%, E₀ 90%, hummock height 20 cm, August 27, 2009, 49° 06.714' ; 19° 48.760' , accuracy 6 m.
4. Liptovská kotlina Basin, Pribylina, Lazy, altitude 796 m a.s.l., totally disintegrated hummock, area 1.5 x 0.5 m, E aspect, inclination 2° , total cover 90%, E₁ 85%, E₀ 70%, hummock height 10 cm, August 27, 2009, 49° 06.730' ; 19° 48.777' , accuracy 6 m.
5. Liptovská kotlina Basin, Pribylina, Lazy, altitude 792 m a.s.l., area 0.7 x 0.7 m, E aspect, inclination 2° , total cover 100%, E₁ 80%, E₀ 80%, hummock height 20 cm, August 27, 2009, 49° 06.703' ; 19° 48.785' , accuracy 8 m.
6. The High Tatra Mts, Christlová raised bog, 1,121 m a.s.l., area 0.6 x 0.8 m, plane, total cover 100%, E₁ 70%, E₀ 100%, hummock height 35 cm, August 17, 2009, 49° 09.770' ; 20° 14.479' , accuracy 7 m.
7. The High Tatra Mts, Christlová raised bog, 1,121 m a.s.l., area 1.0 x 1.0 m, plane, total cover 60%, E₁ 60%, E₀ 60%, hummock height 35 cm, August 17, 2009, 49° 09.760' ; 20° 14.497' , accuracy 6 m.
8. The High Tatra Mts, Christlová raised bog, 1,121 m a.s.l., area 1.0 x 0.7 m, plane, total cover 100%, E₁ 70%, E₀ 100%, hummock height 30 cm, August 17, 2009, 49° 09.762' ; 20° 14.503' , accuracy 7 m.

both rich fen and raised bog habitats show a convergent development, leading to structures dominated by *Calluna vulgaris* with a moss layer dominated by *Pleurozium schreberi*. The residual occurrence of *Polytrichum strictum* and *Sphagnum capillifolium* in some relevés is evidence of turf hummocks origination (Table 8).

Discussion and Conclusions

The key process in the formation of turf hummocks is transition to the ombrotrophic condition. This sequence is accompanied by higher rates of peat accumulation and increasing acidity. This transition may be a consequence of external changes, such as climatic alteration (increased precipitation/evaporation ratio) or autogenic, internal successional developments (Moore 1995). Deposition of 1,804g dry weight of peat can bring about a complete transformation of one square metre of extreme rich fen to bog in all its characteristics (Bellamy and Reiley 1967). The acidity of water in poor fens and bogs is largely due to *Sphagnum* removing metal cations from the water and leaving hydrogen ions as the predominant cations in solution (Raible 2004). The ability of non *Sphagnum* species to lower pH of marsh water facilitates succession from alkaline marsh to *Sphagnum* bog (Glime *et al.* 1982). Because of increasing acidity, the brown mosses of Amblystegiaceae in rich fens are gradually replaced by *Sphagnum* species and peat accumulation causes the peatland surface to become more and more

separated from the direct influence of mineral-rich groundwater (Hájková and Hájek 2004). The result is a spatial mosaic of minerotrophic fens and hummocks, overhanging up to 70 cm, described e.g. by Hájková and Hájek (2004).

Accounts of the suspected sequence of development of these turf hummocks in alpine level from the initial colonization of a suitable substratum to the eventual formation of a turf hummock have been given by Jeník (1958) on seepage NNE steep slope in West Tatra Mts, covering an area of 2 ha. The moisture source on exposed slopes are derived from melting snow, which persist until the end of May (Šibík *et al.* 2006) along with intense precipitation. Because of the decline in decomposition rate on north facing slopes, raw humus is accumulated. The component species occupy wet depressions, leading ultimately to the development of turf hummocks (raised bogs). Initial colonization is generally by invasion of *Sphagnum capillifolium* and *Polytrichum strictum* carpets, with subsequent establishment of phanerophytes among them. Turf hummocks are regarded as cryogenic phenomena, in both rich fens or in raised bogs where decline in decomposition rate induces their inclusion in these ecosystems. An example are incipient turf hummocks closely mirroring surface of the frost table in the Mackenzie delta (Gill 1973).

The occurrence of mixed mires in the Carpathians has been rarely reported, with general mention of *Sphagnum fuscum* hummocks found in calcium – rich fens in the Liptov basin came from Rybníček (Hájková and Hájek 2004). The same authors (Hájková and Hájek 2004) analysed from an ecological point of view a mixed mire at Havraník located in Muránska planina Mts (Central Western Carpathians, Slovakia). The site is composed of mineral rich pools alternating with hummocks up to 70cm height co-dominated by *Sphagnum rubellum* and *Polytrichum strictum*. Hájková *et al.* (2006) described similar *Sphagnum* dominated poor fen community in the Bulgarian mountains (*Bruckenthalio – Sphagnetum capillifolii*), the community being placed in the alliance *Sphagno recurvi – Caricion cannescentis*.

We are not sure that the ordering of *Sphagnum – Polytrichum* hummocks within alliance *Empetrium hermaphroditi* is correct. The strongly deviating nutritional ecology of *Sphagnum* mosses clearly distinguishes fens and bogs from other ecosystems (Aerts *et al.* 1999). At the alpine level, nutritional ecology of turf hummocks strictly separates turf hummocks from adjacent plant communities of the alliance *Empetrium hermaphroditi* (or *Juncion trifidi* respectively), even they erode in their environment and often are classified within these syntaxa (cf. Dúbravcová *et al.* 1976, Šibík *et al.* 2006). From a phytocoenological point of view, the *Sphagnum* rich communities were only partly understood. In Temnosmrečinová dolina Valley (The High Tatra Mts) similar structures were described Hadač (1956). The author introduced two associations dominated by peat mosses: (1) *Sphagneto – Caricetum pauciflorae* with *Sphagnum compactum*, *S. squarosum*, *S. capillifolium*, *S. magellanicum* and *S. robustum* in floristic composition and (2) *Sphagneto – Tricho-*

phoretum alpini dominated by *Sphagnum compactum*. Both the associations were placed by the author in the alliance *Sphagnion fusci* Br.-Bl. 1926, ordo *Sphagnetalia* Pawl.-Skol.-Wallisch 1928. Nevertheless, these communities are without developed turf hummocks. A similar peat moss community under the name *Sphagno - Empetretum hermaphroditi* was described Unar *et al.* (1985) in Tomanova dolina Valley, The West Tatra Mts. These growths occurring at the altitude 1,700 – 1,770 m a.s.l., covering NNE slopes are dominated by *Sphagnum girgensohnii* and *S. robustum*, rarely by *S. magellanicum*, and *Polytrichum strictum* is absent. The author placed this peat moss community into the alliance *Loiseleurio - Vaccinion* Br.-Bl. In Br.-Bl. et Jenny ex Kraj. 1933 (*Loiseleurio - Vaccinieta* class). This community are without created hummocks.

According to Šibík *et al.* (2006), the communities described by Unar *et al.* (1985) or Hadač (1956) creates the connecting link between the alliances *Vaccinion myrtilli* Krajina 1933 and *Oxycocco - Empetrium hermaphrodity* Naordhagen ex Hadač and Váňa 1967. These communities rich in *Sphagnum* species are without developed turf hummocks. The obstacle for inclusion into the alliance *Oxycocco - Empetrium hermaphrodity* is the absence of species *Drosera rotundifolia*, *Eriophorum vaginatum*, *Ledum palustre* and *Oxycoccus palustris* (Šibík *et al.* 2006). Terrain configuration and altitude don't allow occurrence of mentioned species in these structures. Despite the fact that *Polytrichum strictum*, *Sphagnum capillifolium*, *S. magellanicum* are listed as characteristic species of the *Oxycocco - Sphagnetea* (Šoltés *et al.* 2001), there is a lack of analytical material to make more decisive conclusions on phytocoenological ordination of alpine turf hummocks.

Marini *et al.* (2008) analysed the hydrochemistry of a mixed mire in relation to habitat conditions in the Southern Alps. The authors found that in *Sphagnum* hummocks significantly lower concentrations of both anions and cations than are determined for the West Carpathians *Sphagnum* hummocks (Table 2). Karlin and Bliss (1984) studied the chemistry of the upper peat layers of the hummocks and hummock plant community composition in strongly minerotrophic, moderately minerotrophic, and weakly minerotrophic peatland systems in central Alberta. They found similarity in both the chemistry and plant composition independent of calcium carbonate content in the peat substratum. This corresponds with our observations. The chemistry of the catotelm of the mature turf hummocks developed in the strongly minerotrophic peatland system near Dobšinská Ladová jaskyňa is in agreement with the catotelm chemistry of the hummocks developed in the raised bog environment (Table 2, Fig. 3). Convergent development results in similar structures – turf hummocks, independent of the substratum. These structures occupy rich fens of the class *Scheuchzerio - Caricetea fuscae* Tx 1937, oligotrophic raised bogs of the class *Oxycocco - Sphagnetea* Br. - Bl. et R. Tx. 1941 or alpine communities of the class *Loiseleurio - Vaccinieta* Egger ex Schubert 1960. The *Polytrichum strictum - Sphagnum capilli-*

folium hummocks developed on fens or raised bogs are regarded as semi-ombrogenous deriving moisture from precipitation but also relying on ground water in the early stages of their development. The key role belongs to *Sphagnum capillifolium*, this turf moss occupies a wide niche, grows under forest canopy, in rich fens, in poor fens, in raised bogs or in alpine heaths. In extreme acid habitats this turf moss may be replaced by *Sphagnum rubellum*.

Vegetation classification reflects wide altitudinal and ecological gradients influencing species composition. It is not surprising that associated species, invading from adjacent environments have a high fidelity. Thus, hummocks originating in raised bogs are differentiated by the presence of raised bog species such as *Eriophorum vaginatum* and others, whereas hummocks originating in rich fens are characterized by the presence of species such as *Tomentypnum nitens*, *Galium uliginosum*, *Molinia caerulea* and others. These species occupy mainly marginal or basal parts of hummocks, rarely the apical parts, isolated from the peat substrate.

Integrated features are:

1. Co-dominance by moss species *Sphagnum capillifolium* (*S. rubellum* respectively) and *Polytrichum strictum*
2. Conjoint genesis in different ecosystems due to decline in decomposition rate
3. Ombrotrophy
4. Separation from the substrata

Hájková and Hájek (2004) consider the hummock vegetation as ombrotrophic bog communities, although the hummocks may be located in rich-fen vegetation. We think the hummock communities are related more to raised bog vegetation than to the alpine class *Loiseleurio-Vaccinieta* or mire class *Scheuchzerio-Caricetea fuscae*, despite the absence of some raised bog species in the communities confined to alpine level (cf. Šibík *et al.* 2006). Because of the lack of analytical material, these structure are tentatively left in the alpine class *Loiseleurio-Vaccinieta*. It is concluded here that these units developed in rich fens and raised bogs should not be distinguished as separate syntaxa and their evaluation within one vegetation unit (association) is suggested. These structures are specific raised bog communities and should be placed in the class *Oxycocco - Sphagnetea* Br. - Bl. et R. Tx. ex Westhoff *et al.* 1946 as a separate unit within the alliance *Oxycocco-Empetrium hermaphrodity* Nordhagen 1936, the new association *Vaccinio vitis-idaei - Sphagnetum capillifolii*. The alliance *Oxycocco-Empetrium hermaphrodity* includes raised bog communities dominated by chamaephytes, and is widespread from the montane belt up to the subalpine belt, descending down to the submontane basins as isolated hummocks within the complexes of minerotrophic mires (Šoltés *et al.* 2001).

In floristical composition of juvenescent hummocks in rich fen *Polytrichum strictum* is absent. Older hummocks harbour *Sphagnum rubellum*, when *Sphagnum capillifolium* is replaced by this more acidophilous peat moss. Lichens and *Pleurozium schreberi* usually cover, often in high abundance, disintegrated hummocks in the moss

layer and *Calluna vulgaris* frequently dominates among chamaephytes.

Western Carpathians turf hummocks represent a good starting point for further research, as well as for conservation-biological activities.

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References

- Aerts, R., Verhoeven, J.T.A. and Whigham, D.F. 1999: Plant-mediated controls on nutrient cycling in temperate fens and bogs. *Ecology*, **80**: 2170-2181.
- Barkman, J.J., Doing, H. and Segal, S. 1964: Kritische Bemerkungen und Vorschläge zur quantitativen Vegetationsanalyse. *Acta Bot. Nederl.*, **13**: 394-419.
- Bellamy, D.J. and Rieley, J. 1967: Some ecological statistics of a "miniature bog". *Oikos*, **18**: 33-40.
- Braun-Blanquet, J. 1964: Pflanzensoziologie. Grundzüge der Vegetationskunde. Ed. 3. Springer-Verlag, Wien, New York.
- Cykowska, B. 2006: *Sphagnum-Polytrichum* hummocks - noteworthy habitat for liverworts. In: *Tatrzanski Park Narodowy na tle Innych Górskich Terenów Chronionych* (eds. Z. Mirek Z. and B. Godzik), **2**: 63-66.
- Cykowska, B. 2009: Wątrobowce (Hepaticae) kępy Torfowcowo-Płonnikowych w Tatrach - Różnorodność, Rozmieszczenie i Ekologia. Thesis, Institute of Botany, Polish Academy of Sciences. Kraków.
- Cykowska, B. 2011: Bryophytes of *Sphagnum-Polytrichum* hummocks in the Polish Tatra Mountains. In: *Chorological studies in the Polish Carpathians* (eds. A. Stebel and R. Ochrya), in press, Sorus, Poznań.
- Driscoll, C.T. 1984: A procedure for the fractionation of aqueous aluminium. *Intern. J. Environ. Anal. Chem.*, **16**: 267-284.
- Dúbravcová, Z., Foltínová, J., Pačlová, L. and Turečková, J. 1976: Vegetácia subalpínskeho a alpínskeho stupňa Západných Tatier. Final report, mns. [Depon. in Prírodovedecká fakulta UK, Bratislava].
- Ditě, D., Hájek, M. and Hájková, P. 2007: Formal definitions of Slovakian mire plant associations and their application in regional research. *Biologia*, **62**: 400-408.
- Ellenberg, H., Weber, H.E., Düll, R., Wirth, W., Werner, W. and Paulißen, D. 1992: Zeigerwerte von Pflanzen in Mitteleuropa. Ed. 2. *Scr. Geobot.*, **18**: 1-258.
- Fenton, J.H. and Smith, R.I.L. 1982: Distribution, composition and general characteristics of the moss banks of the maritime Antarctic. *British Antarctic Survey Bulletin*, **51**: 215-236.
- Gill, D. 1973: Ecological modifications caused by removal of tree and shrub canopies in the Mackenzie delta. *Arctic*, **26**: 95-111.
- Glime, J.M. 2007: Bryophyte Ecology. Volume 1. Physiological Ecology. Ebook sponsored by Michigan Technological University and the International Association of Bryologists. <http://www.bryoecol.mtu.edu/>. (retrieved 11. 1. 2010).
- Glime, J.M., Wetzel, R.G. and Kennedy, B.J. 1982: The effects of bryophytes on succession from alkaline marsh to *Sphagnum* bog. *Am. Mid. Nat.*, **108**: 209-223.
- Gunnarsson, U. 2005: Global patterns of *Sphagnum* productivity. *Journal of Bryology*, **27**: 269-279.
- Hennekens, S.M. and Schaminée, J.H.J. 2001: TURBOVEG, a comprehensive data base management system for vegetation data. *J. Veg. Sci.*, **12**: 589-591.
- Hadač, E. 1956: Rostlinná společenstva Temnosmrečínové doliny ve Vysokých Tatrách. *Biol. Práce Slov. Akad. Vied*, **21**: 1-78.
- Hájková, P. and Hájek, M. 2004: *Sphagnum*-mediated successional pattern in the mixed mire in the Muránska planina Mts (Western Carpathians, Slovakia). *Biologia*, **59**: 65-74.
- Hájková, P., Hájek, M. and Apostolova, I. 2006: Diversity of wetland vegetation in the Bulgarian high mountains, main gradients and context-dependence of the pH role. *Plant ecology*, **184**: 111-130.
- Horáková, M., Litsche, P. and Grünwald, A. 1989: Chemické a fyzikálne metódy analýzy vod. Praha.
- Jeník, J. 1958: Rašelinové kopčeky v oblasti Veľkej Kopy (2 053 m) vo Vysokých Tatrách. *Sborník Prác o Tatranskom Národnom Parku*, **2**: 30-40.
- Karlin, E.F. and Bliss, L.C. 1984: Variation in substrate chemistry along microtopographical and water-chemistry gradients in peatland. *Can. J. Bot.*, **62**: 142-153.
- Kubinská, A. and Janovicová, K. 1998: Bryophytes. In *Checklist of non-vascular and vascular plants of Slovakia*. (eds. K. Marhold and F. Hindák), pp. 297-332. Veda, Bratislava.
- Klama, H. 2004: Wątrobowce (Marchantiophyta) Babiogórskiego Parku Narodowego. In: *Babiogórski Park Narodowy. Monografia przyrodnicza* (eds. B.W. Wołoszyn, A. Jaworski and J. Szwagrzyk), pp. 333-356. Komitet Ochrony Przyrody PAN i Babiogórki Park Narodowy, Kraków.
- Lamers, L.P.M., Farhoush, C., van Groenendael, J.M. and Roelofs, J.G.M. 1999: Calcareous groundwater raises bogs; the concept of ombrotrophy revisited. *Journal of Ecology*, **87**: 639-648.
- Marhold, K. 1998: Ferns and flowering plants. In *Checklist of non-vascular and vascular plants of Slovakia*. (eds. K. Marhold and F. Hindák), pp. 333-687. Veda, Bratislava.
- Marini, L., Nascimbene, J., Scotton, M. and Klimek, S. 2008: Hydrochemistry, water table depth and related distribution patterns of vascular plants in a mixed mire. *Plant biosystems*, **142**(1): 79-86.
- Matuszkiewicz, W. 2006: Przewodnik do oznaczania zbiorowisk roślinnych Polski. PWN, Warszawa.
- Moore, P.D. 1995: Biological processes controlling the development of modern peat-forming ecosystems. *International Journal of Coal Geology*, **28**: 99-110.
- Raible, B. 2004: White rock fen. *Kalmiopsis*, **11**: 30-35.
- Raup, H.M. 1966: On the structure and development of turf hummocks in the Mesters Vig district, Northeast Greenland. Permafrost International Conference. *National Research Council Publication*, **1287**: 43-50.
- Scotter, G.V. and Zoltai, S. C. 1982: Earth hummocks in the Sunshine Area in the Rocky Mountains, Alberta and British Columbia. *Arctic*, **35**(3): 411-416.
- Seppala, M. 2002: Stratigraphy, age and formation of peaty earth hummocks (pounus), Finnish Lapland. *The Holocene*, **12**(2): 187-199.
- Sillinger, P. 1933: Monografická studie o vegetaci Nizkých Tater. Orbis, Praha.
- Szwejkowski, J. 1960: *Orthocaulis binsteadii* (Kaalaas) Buch – a new liverwort for Central Europe. *Fragm. Flor. Geobot.*, **6**(3): 399-405.
- Szwejkowski, J. and Buczkowska, K. 2000: *Sphagnum-Polytrichum* hummocks – a bryologically neglected plant formation. *Fragm. Flor. Geobot.*, **45**: 475-484.
- Šibík, J., Kliment, J., Jarolímek, I., Dúbravcová, Z., Bělohávková, R. and Pačlová, L. 2006: Syntaxonomy and nomenclature of the alpine heaths (the class *Loiseleurio-Vaccinietea*) in the Western Carpathians. *Hacquetia*, **5**(1): 37-71.
- Šibík, J., Ditě, D., Šibíková, I. and Pukajová, D. 2008: Plant communities dominated by *Pinus mugo* agg. in Central Europe – comparison of the oligotrophic communities rich in *Sphagnum*. *Phytocoenologia*, **38**(3): 1-18.

- Šmarda, J. 1960: Reliktní společenstvo s převládající *Carex paniculata* v Západních Tatrách. *Biológia*, **15**(5): 344-353.
- Šoltés, R., Hájek, M. and Valachovič, M. 2001: *Oxycocco-Sphagneteta*. In: *Rastlinné spoločenstvá Slovenska. 3. Vegetácia mokradí* (ed. M. Valachovič), pp. 275-296. Veda, Bratislava.
- Tarnocai, C. and Zoltai, S.C. 1978: Earth hummocks of the Canadian Arctic and Subarctic. *Arctic and Alpine Research*, **10**: 581-594.
- Ter Braak, C.J.F. and Šmilauer, P. 2002: CANOCO reference manual and CanoDraw for Windows user's guide. Software for canonical community ordination (version 4.5). Biometris, Wageningen & České Budějovice.
- Thompson, M.V., Randerson, J.T., Malmström, C.M. and Field, C.B. 1996: Change in net primary production and heterotrophic respiration: how much is necessary to sustain the terrestrial carbon sink? *Global Biogeochemical Cycles*, **10**: 711-726.
- Tichý, L. and Holt, J. 2006: Juice, program for management, analysis and classification of ecological data. Vegetation Science Group, Masaryk University, Brno.
- Unar, J., Unarová, M. and Šmarda, J. 1985: Vegetační poměry Tomanovy doliny a Žlebu spod Diery v Západních Tatrách. 2. Charakteristika přírodních poměrů a rostlinných společenstev. *Folia Fac. Sci. Nat. Univ. Purkynianae Brun., Ser. Biol.*, **26**(14): 5-78.
- Van den Maarel E. 1979. Transformation of cover-abundance values in phytosociology and its effect on community similarity. *Vegetatio*, **39**: 97-114.
- Vitt, D.H., Halsey, L.A., Campbell, C., Bayley, S.E. and Thormann, M.N. 2001: Spatial patterning of net primary productivity in wetlands of continental western Canada. *Écoscience*, **8**: 499-505.
- Weber, H.E., Moravec, J. and Theurillat, J.-P. 2000: International Code of Phytosociological nomenclature. Ed. 3. *J. Veget. Sci.*, **11**: 739-768.
- Westhoff, V. and van den Maarel, E. 1978: The Braun-Blanquet approach. In *Classification of plant communities*. (ed. R.H. Whittaker), pp. 289-399. W Junk, The Hague.
- Wildi, O. and Orlóci, L. 1996: Numerical Exploration of Community Patterns. A guide to the use of MULVA-5. 2nd edition. SPB Academic Publishing b.v., Amsterdam.

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