The occurrence of the relict plant, *Trichophorum pumilum*, in the Western Carpathians in the context of its distribution and ecology in Eurasia

Výskyt reliktního druhu *Trichophorum pumilum* v Západních Karpatech v kontextu jeho rozšíření a ekologie v Eurasii

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Dedicated to Kamil Rybníček and Eliška Rybníčková on the occasion of their 80th birthdays

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Vascular-plant relict species *Trichophorum pumilum* has a disjunct distribution range and in Europe (not considering Caucasus and South Ural Mts) it currently occurs only in the Alps, Norway and a small area in the Western Carpathians. This study reviews all available data on the distribution and ecology of this species in Europe, provides vegetation and ecological characteristics of recent populations in the Western Carpathians and compares them with that found in other European regions. In the Western Carpathians this species is found in a small area in an Inner-Carpathian basin in northern Slovakia, the Liptov, Poprad and Hornád Basin, and rarely reaches the margins of adjacent mountains. It is currently present at 10 sites in this area. This species is therefore classified in the IUCN category "endangered". Occurrence of *Trichophorum pumilum* is associated with calcareous fens, usually those initiated during the late glacial and surrounded by extremely mineral-rich active travertine springs. Finds of macrofossils suggest that the species was more widespread in Europe and Slovakia during the last glacial. Currently this species occurs in communities of the *Caricion davallianae* alliance, associations *Glauco-Trichophoretum pumili* and *Caricetum davallianae*. Habitat and vegetation affinity differ substantially from that found at most other European localities of this species. The reasons for this difference are the specific ecological conditions of travertine springs and surrounding fens, which enabled the postglacial survival of this species at rather low altitudes in the temperate zone. One of the most important differences is the occurrence of halophytic and subhalophytic species at the Western-Carpathian localities, which makes their vegetation somewhat analogous to that of *T. pumilum* fens found in the Russian Altai Mts. We demonstrate this similarity by detrended correspondence analysis of all available individual relevés from the Carpathians, the Alps and Altai.

K e y w o r d s: calcareous fen vegetation, Europe, halophyte, macrofossils, postglacial relict, recent distribution, threatened plants, travertine

Introduction

The genus *Trichophorum* (*Cyperaceae*) consists of three boreal-mountain species in Europe: *Trichophorum cespitosum*, *T. alpinum* and *T. pumilum*. All have circumpolar distributions (Hultén & Fries 1986) and relict distributional patterns in central Europe (e.g. Hájek et al. 2011). *Trichophorum pumilum* is the rarest and despite its extraordinary distribution pattern in Europe, data on its ecology, history and vegetation preferences are rather scarce. The distribution of *T. pumilum* [bas.: *Scirpus pumilus* Vahl, syn.: *Baeothryon pumilum* (Vahl) Á. Löve et D. Löve; *Eriophorella pumila* (Vahl) Kit Tan, *Scirpus atrichus* (Palla) Dalla Torre et Sarnth. non Poir., nom. illeg.; *Trichophorum atrichum* Palla; *Trichophorum oliganthum* (C. A. Mey.) Fritsch.] is viewed as either Siberian-North American (Aeschimann et al. 2004), arctic-alpine (Máthé 1940) or boreal-continental-Eurasian (Dostál 1992). In North America, it occurs in western Canada and adjacent territory in Alaska, in north-eastern Canada and in the Rocky Mts and Sierra Nevada Mts in the U.S.A. (Hultén & Fries 1986, Cooper 1995, USDA NRCS 2013). In Asia, *T. pumilum* occurs from Iran in the southwest (the wetland "green islands" in the Alborz Mts; Naqinezhad et al. 2009) through Central-Asian Mountains (Tian-Shan, Himalayas, Altai) and southern and south-western Siberia to Mongolia in the east (valley meadow fens in the steppe zone; Minayeva et al. 2005). In Europe, *Trichophorum pumilum* has a disjunct distribution. It occurs in Norway, from where it is known from two isolated regions: one located north of the Arctic Circle (Tromsø, Finnmark) and the other in the mountains of southern Norway (the Rondane and Dovrefjell Mts). This species has been found in the western and southern Alps (France, Switzerland and Italy). Its occurrence in easternmost Europe represents the margin of a more connected Asian distribution range (Hultén 1958, Engelskjøn & Skifte 1987, Song-Jun & Tucker 2010). In central Europe outside the Alps it occurs in a small isolated area in the Western Carpathians (Slovakia). The ecological amplitude of *Trichophorum pumilum* there is very narrow and the species is rare. It is reported from calcareous fens and travertine swards that develop around mineral-water springs in intermountain basins (Šmarda 1961, Vicherek 1973, Hájek et al. 2011).

The main objectives of this paper are to: (i) compare the historical and current distribution of *Trichophorum pumilum* in the Western Carpathians, and (ii) present the vegetation and ecological characteristics of Western-Carpathian populations and compare them with those in other parts of its Eurasian distribution range.

Material and methods

The study was carried out from 2001–2012 in Slovakia. The data concerning the distribution of the species was obtained from specimens in herbaria BP, BRA, BRNM, BRNU, CL, NI, PR, PRC, SAV, SLO and ZV. Herbarium abbreviations are according to Holmgren & Holmgren (1998) and Vozárová & Sutorý (2001). Coordinates of recent localities were obtained during field research using GPS equipment Garmin CS 60; the numbers of grid squares follow one that was described by Niklfeld (1971). Results are presented as a map created using ArcGis software, version 9.2. A list of localities was compiled according to the actual directives of the Flora of Slovakia (Goliašová & Michalková 2012). Phytogeographical division follows Futák (1980). The Red-List status was assessed using IUCN categories and criteria (IUCN 2001).

Phytosociological relevés (vegetation-plot records) were sampled according to the Zürich-Montpellier approach using the adapted nine-degree Braun-Blanquet's scale (Barkman et al. 1964). Nomenclature of vascular plants follows Tutin et al. (1964–1980). The nomenclature of bryophytes follows Hill et al. (2006). The author and year of description of syntaxa used in the paper are quoted with the first reference.

Values of pH and electrical conductivity were measured directly at the site in the ambient water using a CyperScan PC 300. The conductivity values are those for a temperature of 20 °C. The hydrogen-ion-based conductivity was subtracted (Sjörs 1952).

The phytosociological relevés were compared with 41 relevés from the Alps (one relevé from Friedel 1956, 34 from Steiner 2002, two unpublished relevés of L. Sekulová analysed in Sekulová et al. 2013 and four of our unpublished relevés) and nine from the Altai (unpublished relevés of M. H., P. H., J. Danihelka and M. Chytrý, for details see Horsák et al. 2010). We used detrended correspondence analysis (DCA), with downweighting of rare species. Floating cut levels were used, i.e. cover values were converted either to 1 if they were lower than the median non-zero cover of the species in the entire data set, or to 2 if it was equal or higher than the median value. *Trichophorum pumilum* was passive in the analysis. Data from Norway were not included in this analysis, because there are no full relevés published for this country.

Results

The distribution of Trichophorum pumilum in the Western Carpathians

Trichophorum pumilum is a very rare species in the Western Carpathians. It has been reported from 23 localities (Electronic Appendix 1) in 21 mapping quadrats (Fig. 1). Herbarium specimens from only 13 localities were found during our research. These localities are concentrated in a small area of inner basins in northern Slovakia – the Liptov, Poprad and Hornád Basins. This distribution range ends at the margin of adjacent mountains, with few localities in the foothills of the Veľká Fatra Mts and the Nízke Tatry Mts. An isolated mountain occurrence is documented for the Slovenský raj Mts. Of these 13 reliably documented localities three were not confirmed recently. Calcareous fens near the Stratenská Píla settlement (Slovenský raj Mts) and near the Liptovský Ján village (Nízke Tatry Mts) have been destroyed; the former was flooded by the Dedinky dam, while the latter was drained. The third locality specified as "fen meadows close to Šarpanec" (cf. Electronic Appendix 1) was never confirmed despite an intensive search of all fens in this region. The current existence of the 10 other localities was confirmed during our field research (Electronic Appendix 1). A brief description of habitat and population characteristics of *T. pumilum* is as follows:

(i) Stankovany village, the Močiar Nature Reserve. *Trichophorum pumilum* population is scattered in various places in the central part of the fen, altogether covering an area of ~50 m^2. (ii) Rojkov village, the Rojkovské rašelinisko Nature Reserve. A small population persists in a central, strongly waterlogged patch around a mineral water spring; total area occupied is ~150 m^2. (iii) Bešeňová, north of the village. After the destruction of a large travertine area at the beginning of 1970s, two small populations still survive in the vicinity of the last active travertine cascade in the Červená terasa Nature Reserve; *Trichophorum pumilum* persists in patches directly affected by mineral spring water in an area of ~80 m^2.

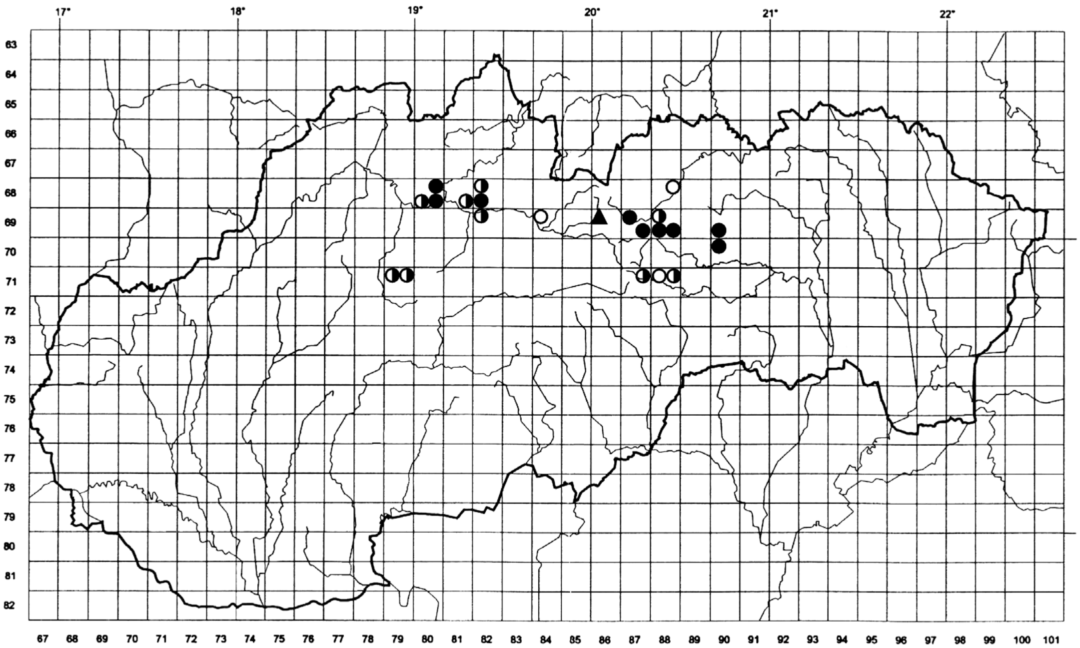

Fig. 1. - Occurrence of *Trichophorum pumilum* in Slovakia: ○ historical localities documented by herbarium voucher specimens, ● recently confirmed localities documented by herbarium voucher specimens, ◑ data from literature, ▲ macrofossil record.

(iv) Spišská Teplica, south-eastern edge of the village. After drainage of fens between the towns of Poprad and Spišská Teplica, the species survives only in a fragment of damaged fen in an area of about 30 m^2. (v) Gánovce village, abandoned travertine quarry. *Trichophorum pumilum* grows along the mineral water stream flowing from a spring in the quarry; a small population grows on newly forming traverine and occupies an area of 3 m^2 at most. (vi) Gánovce, east of the village on the left bank of the Gánovský potok brook, close to the Briežky Nature Reserve. Two populations occur there. The first is rather abundant and grows in a mineral-rich spring fen of about 1500 m^2 in area. The second is ~200 m distant, is very small and occurs along a mineral-water stream in the Briežky Nature Reserve. (vii) Hôrka, the north-eastern margin of the village, close to the main road from Poprad to Levoča. The population grows in remnants of fen, occupying an area of ~1000 m^2. (viii) Hôrka, the eastern edge of the village. This population is situated directly in the village, ~300 m from the previous one. *Trichophorum pumilum* grows in a small shallow-valley fen on the right bank of the Tarnovský potok brook, covering an area of ~1500 m^2. (ix) Baldovce village. A very small population persists in small remnants of ancient travertine swards around springs of mineral water on the eastern edge of the village. This population occupies an area of ~15 m^2. (x) Sivá Brada travertine. This population is the largest in the Western Carpathians. It is formed by four subpopulations growing around individual mineral springs in the foothills of a travertine cone; the most abundant one is located in the western foothills. The total area occupied by this species is ~4500–5000 m^2. The next ten localities are published without herbarium evidence (Fig. 1, Electronic Appendix 1; for details see Discussion) and have not been confirmed recently.

Based on the data presented, we can confirm that this species has Red-List status “endangered” [EN B2a(i)b(iii)] in Slovakia, because its occurrence there is fragmented into small populations, which are threatened by changes in water regime and secondary succesion.

Trichophorum pumilum communities in the Western Carpathians

In the Western Carpathians, we found *Trichophorum pumilum* only in calcareous fens and travertine swards at altitudes between 430–700 m a.s.l. (Table 1). The vegetation belonged to the *Caricetum davallianae* Dutoit 1924 and *Glauco-Trichophoretum pumili* Vicherek 1973 associations, which both belong to the *Caricion davallianae* Klika 1934 alliance (Dítě et al. 2007),

The *Glauco-Trichophoretum pumili* association is characterized by a high dominance of *Trichophorum pumilum* (30–50% on average) and a frequent occurence of obligate (*Glaux maritima*, *Triglochin maritima* and *Plantago maritima*) and facultative (*Carex distans*, *Centaurium littorale* subsp. *uliginosum* and *Schoenoplectus tabernaemontani*) halophytes, whose occurence mirrors a high content of dissolved salts, especially sulphates. In addition, several species of calcareous fens (*Eleocharis quinqueflora*, *Epipactis palustris*, *Pedicularis palustris*, *Primula farinosa* and *Pinguicula vulgaris*) characterize this vegetation. The indicator bryophyte species are *Campyliadelphus elodes* and, on the Sivá Brada travertines, *Bryum maratti* (Šoltés et al. 2010) and *B. neodamense* (Table 2, relevés 5–9). At the most extreme sites of newly precipitated travertine, bryophytes do not occur and cover of vascular plants is only about 20% (Table 2, rel. 9). This association represents the most extreme end of the poor-rich fen gradient, being even more calcium- and magnesium-rich than most other calcareous fens. Water conductivity reaches much higher values than in peat-forming calcarous fens, from 2000 to 4500 (6000) $\mu S \cdot cm^{-1}$. The pH range is 6.5–7.7, indicating a neutral to alkaline reaction (Table 1). Unequivocally classified stands of this association occur only in the Poprad and Hornád basins.

As compared to the *Glauco-Trichophoretum pumili* association, abundance of *Trichophorum pumilum* is lower in peat-forming calcareous fens of the *Caricetum davallianae* association (cover of ~10%, Table 2, relevés 1–4). Obligate halophytes are represented by *Triglochin maritima* and several subhalophytic species identical with the *Glauco-Trichophoretum pumili* association (Table 2). Water conductivity was typically around 1000 $\mu S \cdot cm^{-1}$, pH values varied from 6.3 to 7.1 (Table 1). These values correspond with other *Caricetum davallianae* fens in the Inner-Carpathian basins.

The Bešeňová travertines have a species composition intermediate between the two above mentioned associations (see DCA ordination of the Western-Carpathian relevés in Electronic Appendix 2). Despite the occurrence of both hard travertine and the extremelly high conductivity (4850 $\mu S \cdot cm^{-1}$) *Glaux maritima* and *Plantago maritima* are absent and the vegetation is therefore classified as the *Caricetum davallianae* association (Table 2, relevé 4).

Macrofossil record

There is only a single fossil of this species from the Western Carpathians, which is reported for the first time in this paper. P. H. found 12 seeds of *T. pumilum* in four samples

Table 1. – Recent localities of *Trichophorum pumilum* in the Western Carpathians.

Location	Altitude [m]	Substrate	Vegetation	pH	Conductivity [µS·cm^{-1}]
Veľká Fatra Mts:					
Rojkovské rašelinisko Nature Reserve	435	fen peat with unconsolidated tufa	*Caricetum davallianae*	7.1	590
Stankovany, Močiar Nature Reserve	436	fen peat with unconsolidated tufa, travertine	*Caricetum davallianae*	6.9	1240
Liptovská kotlina Basin:					
Bešeňová	522	travertine cone	*Caricetum davallianae*	6.3	4850
Popradská kotlina Basin:					
Spišská Teplica	700	fen peat with unconsolidated tufa	*Caricetum davallianae*	7.1	670
Gánovce, abandoned travertine pit	620	travertine cone	presence on the felled travertine	*	*
Gánovce, valley	608	fen peat with strong calcium carbonate precipitation	*Glauco-Trichophoretum pumili*	7.3	2620
Hôrka, near the road to Poprad	619	fen peat with strong calcium carbonate precipitation	*Glauco-Trichophoretum pumili*	6.8	4500
Hôrka, Tarnovský potok site	612	fen peat with strong calcium carbonate precipitation	*Glauco-Trichophoretum pumili*	6.5	4010
Hornádska kotlina Basin:					
Sivá brada site	460–490	travertine cone	*Glauco-Trichophoretum pumili*	7.7	4200
Baldovce	434	fen peat with strong calcium carbonate precipitation	*Glauco-Trichophoretum pumili*	*	*
Average	–	–	–	6.96	2834

Table 2. – The phytosociological table of fen vegetation with *Trichophorum pumilum* in the Western Carpathians.

Number of relevé	1	2	3	4	5	6	7	8	9
Area of relevé (m^2)	16	16	16	16	16	16	16	16	16
cover E_1 %	65	85	80	50	75	85	80	75	20
cover E_0 %	90	70	35	5	20	98	90	50	0
Diagnostic taxa of *Caricetum davallianae*									
Epipactis palustris	a	1	a	.	1	1	.	.	.
Campylium stellatum	3	4	b	.	b	.	.	.	.
Parnassia palustris	a	1	.	1	+	1	1	.	.
Pinguicula vulgaris	a	1	.	.	a	.	.	.	.
Primula farinosa	a	a	.	.	1	3	b	.	.
Carex davalliana	a	.	1	.	.	.	.	.	.
Tofieldia calyculata	a	+	.	.	.	.	.	.	.
Diagnostic taxa of *Glauco-Trichophoretum*									
Plantago maritima	.	.	.	.	+	a	a	a	b
Campyliadelphus elodes	.	.	.	.	.	5	5	3	.
Glaux maritima	.	.	.	.	.	1	1	1	.
Other species									
Trichophorum pumilum	1	+	1	a	4	4	1	3	1
Triglochin maritima	1	+	.	b	1	1	1	a	1
Triglochin palustris	+	+	1	1	1	1	1	1	.
Molinia caerulea	a	a	a	r	1	.	.	.	r
Schoenoplectus tabernaemontani	.	1	.	1	b	r	.	a	.
Blysmus compressus	a	.	.	a	.	+	3	1	.
Festuca rubra	1	.	.	+	.	1	1	.	.
Centaurium littorale subsp. *uliginosum*	.	+	.	1	1	.	.	a	
Juncus articulatus	.	1	+	1	1	.	.	.	.
Carex distans	.	.	.	1	+	1	1	.	.
Potentilla erecta	a	1	a	.	.	.	.	.	.
Briza media	.	.	+	+	.	.	1	.	.
Achillea millefolium	.	.	+	.	+	1	.	.	.
Galium verum	.	.	a	+	r	.	.	.	.
Ranunculus acris	.	.	+	.	.	+	1	.	.
Deschampsia cespitosa	.	.	1	.	.	+	.	+	.
Odontites vulgaris	.	.	.	.	.	1	1	1	.
Agrostis stolonifera	.	.	.	1	.	.	.	+	+
Carex nigra	1	.	.	.	.	.	1	.	.
Lotus corniculatus	r	.	r	.	.	.	.	.	.
Equisetum palustre	1	.	1	.	.	.	.	.	.
Valeriana simplicifolia	r	.	1	.	.	.	.	.	.
Polygala amara	+	.	.	r	.	.	.	.	.
Succisa pratensis	.	.	1	r	.	.	.	.	.
Cirsium canum	.	.	1	.	.	+	.	.	.
Carex panicea	.	.	a	.	.	.	1	.	.

Species recorded in only one relevé (vascular plants): *Angelica sylvestris* r (3); *Caltha palustris* 1 (3); *Carex hostiana* 2a (3); *C. lepidocarpa* 1 (1); *C. viridula* r (4); *Cirsium palustre* + (3); *C. rivulare* 2a (3); *Dactylorhiza incarnata* + (6); *Dactylorhiza majalis* 1 (6); *Equisetum arvense* r (4); *E. variegatum* 2a (1); *Eleocharis quinqueflora* 1 (2); *Eriophorum angustifolium* 2a (1); *E. latifolium* r (2); *Galium boreale* 3 (3); *G. palustre* + (3); *Juncus compressus* 1 (7); *J. inflexus* + (3); *Lathyrus pratensis* + (3); *Lotus tenuis* + (1); *Mentha arvensis* + (4); *Menyanthes trifoliata* 1 (1); *Ononis arvensis* + (3); *Pedicularis palustris* 1 (7); *Potentilla anserina* + (4); *Prunella vulgaris* + (3); *Salix rosmarinifolia* 2b (3); *Schoenus ferrugineus* 4 (2); *Taraxacum* sect. *Palustria* r (7); *Trifolium campestre* + (7); *T. fragiferum* subsp. *bonannii* 1 (7); *Trifolium pratense* + (6); *Trifolium repens* 1 (7); *Valeriana dioica* + (1).

Species recorded in only one relevé (bryophytes): *Aneura pinguis* r (5); *Bryum neodnamense* + (8); *B. pseudotriquetrum* 1 (4); *Calliergonella cuspidata* 2a (3); *Scorpidium cossonii* 3 (1); *Fissidens adianthoides* + (1); *Tomentypnum nitens* 2a (1); *Plagiomnium elatum* + (3).

Localities of the reléves: **1.** Veľká Fatra Mts, Stankovany, Močiar Nature Reserve, 49°09'11.8", 19°09'10.5", 18. 6. 2002. **2.** Veľká Fatra Mts, Rojkov, Rojkovské rašelinisko Nature Reserve, 49°08'54.4", 19°09'19.8", 26. 5. 2001. **3.** Popradská kotlina Basin, Gánovce, inundation of the Gánovský potok stream E from the village, left bank, 49°01'25.6", 20°20'05.3", 27. 5. 2003. **4.** Liptovská kotlina Basin, Bešeňová, 49°06'14.9", 19°26'15.2", 26. 6. 2003. **5.** Popradská kotlina Basin, Spišská Teplica, 49°02'37.1", 20°14'36.7", 27. 5. 2003. **6.** Popradská kotlina Basin, Hôrka, E from the village near the road to Levoča, 49°01'16.0", 20°23'44.1", 22. 6. 2004. **7.** Popradská kotlina, Hôrka, near the spring of the Tarnovský potok stream, 49°01'16.0", 20°23'44.1", 22. 6. 2004. **8.** Hornádska kotlina Basin, Sivá Brada, below the western foothills, 49°00'23.9", 20°43'05.9", 2. 6. 2006. **9.** Hornádska kotlina Basin, Sivá Brada, northeastern foothills, 49°00'26.4", 20°44'22.2", 23. 6. 2004.

from the Brezové fen close to Štrba village (890 m a.s.l.; the Liptov basin, see Fig. 1). One sample was dated to between 11,593 and 11,242 BP (calibrated 2δ range; uncalibrated C^{14} date was 9930±30 years; dated material was *Tomentypnum nitens*; AMS method), others were at the same depth or from deeper layers. This result corresponds to the lateglacial/Holocene transition. This species was accompanied by the fen bryophytes *Tomentypnum nitens* and *Scorpidium cossonii*.

Ordination analyses

DCA of available relevés from the Alps, Western Carpathians and Altai produced the principal continentality gradient from the Alps to Altai. The Western-Carpathian relevés occupied a central position, with *Glauco-Trichophoretum pumili* relevés being similar to those from the Altai, and *Caricion davalliane* relevés similar to those from the Alps (Fig. 2). The central position of the Western-Carpathian relevés could be at least partially caused by a high number of species confined only to either the Alps or Central Asia. In order to supress these phytogeographical effects, we repeated the analysis without the species that are geographically confined to only one of the regions studied. This ordination produced the same principal continentality gradient. The groups of relevés from the Carpathians and Altai overlapped along the first (the principal) axis, but were clearly separated along the second axis (Electronic Appendix 3).

Discussion

Distribution in the Western Carpathians

Occurence of *Trichophorum pumilum* in the Western Carpathians is confined to wetlands whose initiation and existence are conditioned by mineral-rich water emerging from springs along numerous geologic breaks in the Inner-Carpathian basins and foothills (Droppa 1975). Travertine is deposited by mineral springs, i.e. it is a fresh water limestone, which precipitates from supersaturated solutions of calcium bicarbonate. Travertines were deposited at the end of the Tertiary and during the interglacial periods of the Quaternary including the Holocene (Kovanda 1971, Novodomec 2006). *Trichophorum pumilum* is currently rare in the Western Carpathians, with reliable records for 13 localities including those already destroyed by man. There is only literature data for the

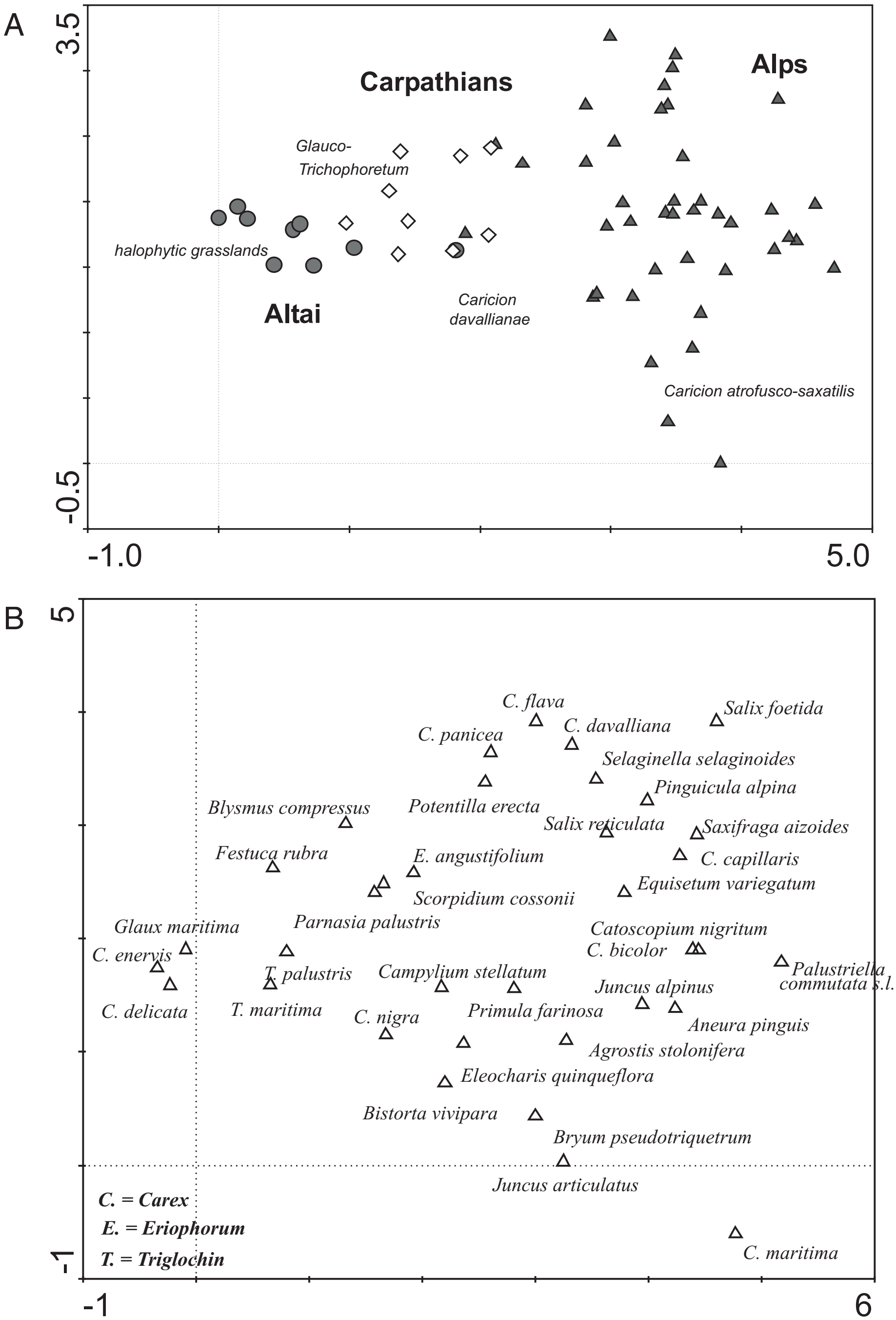

Fig. 2. – DCA ordination of the available relevés from the Western Carpathians, Alps and Altai. Position of sites (A) and species (B) along the first two ordination axes are shown. The eigenvalues of the axes are 0.664 (11% of total inertia) and 0.308 (5.1%). Floating cut levels according to median non-zero cover of a species were used and *Trichophorum pumilum* was passive in the analysis. Only species with the highest weight in the analysis are shown.

Turčianska kotlina basin, where the species is reported from Turčiansky Michal-Háj (Bosáčková 1974), Príbovce (Bosáčková 1974) and Rakšianske rašelinisko (Margittai 1913, Bosáčková 1974). There is a possibility that these reports are incorrect, because of the frequent confusion with *Eleocharis quinqueflora*, which we observed during herbarium revisions. Bosáčková (1974) did not report *E. quinqueflora* even though this species is abundant at the sites she studied. In addition, the fens in the Turčianska basin differ from those at other localities of this species in the absence of travertine or hard calcium carbonate in soil profiles.

Localities that are not documented by herbarium vouchers occur also within the reliably documented distribution of this species. Dítě et al. (2004) report two small populations, from which they did not collect herbarium specimens for conservation reasons. One site is located west of the village of Stankovany, ~300 m from an extant population in the Močiar Nature Reserve. The second is more isolated and in the Sliačske travertíny Nature Reserve; this population was not recently confirmed. Novák (1954) reports the species at the Lúčky spa in the Chočské vrchy Mts. In the Slovenský raj Mts, Šmarda (1970) reports *Trichophorum pumilum* in the surrounding of the Dobšiná Ice Cave and Suza (1946 sec. Pitoniak et al. 1978) at the Veľké Zajfy and Malé Zajfy springs.

Vegetation and ecological characteristics in the Western Carpathians

In the Western Carpathians, the first phytosociological relevés with *Trichophorum pumilum* were published by Šmarda (1961) from the Sivá Brada travertine cone (the Hornád Basin), where vegetation is strongly affected by mineral-rich water with a high concentration of salts, CO_2 and H_2S, as well as compact travertine. Šmarda (1961) identified eight types of vegetation, in which *T. pumilum* occurred not only in wet patches with *Glaux maritima*, but also in less wet but still moist patches dominated by *Plantago maritima*. This author includes both of these types of vegetation in halophytic vegetation (the *Thero-Salicornietea* Tx. in Tx. et Oberd. 1958 class) and points out that they probably represent a separate alliance. Later, Vicherek (1973) did indeed decribe from travertines between the Gánovce and Švábovce villages a new alliance *Halo-Trichophorion pumili* (the *Thero-Salicornietea* class) with a single association *Glauco-Trichophoretum pumili* Vicherek 1973. This association represents a unique community that has not been recorded anywhere else other than the Western Carpathians; our ordination analysis suggests a certain analogy to Altaian *T. pumilum* wetlands, where, however, also strongly continental species such as *Carex delicata* C. B. Clarke or *C. enervis* C. A. Mey. occur (Fig. 2). Dítě et al. (2007) include *Glauco-Trichophoretum pumili* in the *Scheuchzerio palustris-Caricetea nigrae* Tx. 1937 class (alliance *Caricion davallianae*).

Fen vegetation with *T. pumilum* that develops on deposits formed at least partly of peat was distinguished from the mineral-soil plant community of the *Glauco-Trichophoretum pumili* association in the last vegetation survey of Slovakia (Háberová & Hájek 2001). The division of Western-Carpathian *T. pumilum* vegetation into two associations is supported by our ordination analyses.

Relict character of this species distribution

Trichophorum pumilum is considered to be a relict species in the Western Carpathians. The relict character of present-day populations was confirmed by Hájek et al. (2011) who record that the *Trichophorum pumilum* fens were initiated in the late-glacial period, around 10,000 cal. yr BP. For example, the Stankovany fen was initiated ca 12,000 cal. yr BP and the Rojkovské rašelinisko Nature Reserve, the oldest active fen in the entire Western Carpathians, was initiated ca 17,000 cal. yr BP. Statistical testing reveal that recent *T. pumilum* occurrence is significantly linked to ancient fens (Hájek et al. 2011). Our macrofossil record suggests that during the late glacial the species was more widespread, at least in the Liptov Basin. In Europe, this species was probably much more abundant during the last glacial period. Haest et al. (1986) report its occurrence in the sandy region of northern Belgium in the full-glacial period (42,000 uncal. yr BP), ca 700 km from the nearest recent populations in the Alps. This finding underlies the clear recent relict distributional pattern. Indeed, *T. pumilum* is also considered to be a relict species in the Alps (Richard 1991). Engelskjøn & Skifte (1987) speculate that during the Last Glacial Maximum, the species migrated into periglacial areas in Norway, including unglaciated areas on the outermost coast in northern Norway, while in central Europe it persisted in alluvial lowlands in the Alps and Carpathians from where it migrated a few hundred kilometers at most to the nearest high mountain ranges. Our macrofossil finding in the Liptov basin, however, suggests that during the last glacial this species might have been common in intermountain basins at rather high altitudes, which contrary to those in the Alps were not glaciated. The macrofossil found in Belgium (Haest et al. 1986) further suggests that Norwegian and central-European populations were more interconnected than previously implied by Engelskjøn & Skifte (1987).

Comparison with other regions

Most of the available data from the Alps came from the surroundings of Zermatt, Switzerland, from altitudes between 2200 and 2500 m a.s.l., where the species occurs predominantly in the vegetation of the *Caricion atrofusco-saxatilis* Nordhagen 1973 alliance growing on serpentine, Triassic limestones and calcareous shales (Richard 1991, Steiner 2002). Steiner (2002) identified subasociations characterized by *T. pumilum* dominance within *Juncetum arctici* (Gams 1972) Bressoud 1989, *Junco triglumis-Caricetum bicoloris* Doyle 1952 and *Caricetum microglochinis* Nordhagen 1928 associations. Other data for the Alps, also from similar altitudes (1860–2400 m a.s.l.), came from the canton of Engadine (Favre 2006 and own unpublished data), the Mattmark (the Pennine Alps; Yerly 1963) and French Alps (Bournerias 1990, Bornand & Hoffer-Massard 2002). Similar to Steiner (2002), Yerly (1963) and Bournerias (1990) report this species from the *Caricion atrofusco-saxatilis* alliance, characterized by *Juncus arcticus* and *Carex bicolor*. In the canton of Engadine, close to St Moritz, Favre (2006) reports that this species is accompanied by species of calcareous fens and alpine wetlands (e.g. *Carex davalliana*, *Equisetum variegatum*, *Eleocharis quinqueflora*, *Juncus alpinus*, *Kobresia simpliciuscula* and *Tofieldia pusilla*). In the same canton, we recorded *Trichophorum pumilum* on gravel alluvium sediments with shallow soil in an alpine valley close to S-Charl village (unpublished data of D. D., P. H. and M. H.).There was a low cover (up to 5%) there of *T. pumilum* in species-rich initial alpine vegetation, where calcareous-fen species (e.g. *Carex dioica*, *Equisetum variegatum*, *Primula farinosa*, *Pinguicula vulgaris*) co-existed with species of alpine tundra (*Bartsia alpina*, *Salix reticulata*, *Thalictrum alpinum*). All these localities differ from the Western-Carpathian *T. pumilum* habitats in having a high representation of arctic-alpine species.

Some *T. pumilum* fens in the Alps, however, resemble those occurring in the Western Carpathians. Steiner (2002) also records a high cover of *T. pumilum* in the vegetation of the *Caricion davalliane* alliance (the *Caricetum davalliane trichophoretosum pumili* subassociation) in which artic-alpine species diagnostic of the *Caricion atrofusco-saxatilis* alliance are rare. This vegetation is similar to the Western-Carpathian vegetation of the *Caricetum davallianae* association, but lacks subhalophytic species. The DCA ordination (Fig. 2) clumped a few relevés from the Alps together with the *Caricetum davallianae* relevés from the Western Carpathians. Similar vegetation could be expected to occur also in the area of Saint-Dalmas-de-Selvage (Valley de Sagnas, the Maritime Alps Mts, France), from where Bornand & Hoffer-Massard (2002) report *T. pumilum* occurring together with a set of species that also grow in the Western-Carpathian *T. pumilum* fens (*Blysmus compressus*, *Carex davalliana*, *Eleocharis quinqueflora*, *Primula farinosa*). On the other hand, this locality also harbours some species that do not occur in Western-Carpathian vegetation with *T. pumilum* (e.g., *Thalictrum alpinum*, *Trichophorum cespitosum*).

For the Zermatt region, Steiner (2002) reports pH values of *T. pumilum* fens mostly between 6 and 7. We revisited some of Steiner's sites and measured higher pHs, between 7.5 and 7.8; we further measured water conductivity, which varied between 190 and 320 $\mu S \cdot cm^{-1}$ (unpublished data of D. D., P. H. and M. H.). Nevertheless, we found only fens of the *Caricon davallianae* alliance, while fens of the *Caricion atrofusco-saxatilis* alliance seemed to be dissapearing gradually because of water capturing and retreat of glaciers.

The Western-Carpathian vegetation with *T. pumilum* resembles saline fen grasslands and calcareous fens in continental intermountain basins in the central Altai Mts (southern Siberia, Altai Republic, Russian Federation). These two regions are similar in the occurrence of subhalophytic species together with calcareous-fen and grassland species and a lower representation of artic-alpine species (Figure 2). The vascular plant taxa that grow in both Western-Carpathian and Altaian *T. pumilum* wetlands are (sorted by decreasing frequency in nine relevés): *Parnassia palustris* (8), *Triglochin palustris* (7), *Glaux maritima* (6), *Triglochin maritima* (5), *Eleocharis quinqueflora* (5), *Carex nigra* s.l. (3), *Pedicularis palustris* s.l. (2), *Eriophorum angustifolium* (2), *Carex dioica* (1), *Equisetum variegatum* (1) and *Salix rosmarinifolia* (1). Of the above mentioned taxa there are seven of the 11 calcareous fen specialists, which indicate a significant link to older fens that would be expected from their random distribution in the Western Carpathians (Hájek et al. 2011). In even more extreme continental regions of Mongolia, the similarity with Western-Carpathian *T. pumilum* fens decreases, but some species such as *Triglochin maritima* and *T. palustris* are still present (Minayeva et al. 2005). These two species cooccur with *T. pumilum* also in fens in North America (e.g. Cooper 1995).

Norwegian vegetation with *T. pumilum* could not be included in this comparison, but because of the great representation of artic-alpine tundra species and absence of both the halophytic species and the species of continental grasslands it is likely that Norwegian *T. pumilum* vegetation would be placed at the extreme end of the observed principal gradient, behind that of the Alps. Engelskjøn & Skifte (1987) record the vegetational and ecological characteristics of *T. pumilum* in northern Norway, at altitudes between 0 and 70 m a. s. l., where most populations were recorded growing on carbonate rocks, especially Precambrian dolomites. Soil pH varied between 5.7 and 6.8 and floristic composition included species found in the spring-fen relevés from the Alps (*Bistorta vivipara*, *Carex capillaris*, *Pinguicula alpina*, *Thalictrum alpinum*, *Saxifaraga aizoides* and *Tofieldia pusilla*) as well as the rather dryland species *Campanula rotundifolia*, *Carex rupestris*, *Dryas octopetala* and *Festuca ovina*. In addition to these "lowland" locations, *Trichophorum pumilum* grows in wind-eroded *Dryas* turf with some hygrophytes, but also with chionophobous species such as *Carex glacialis*, *Chamorchis alpina*, *Braya linearis*, *Rhododendron lapponicum* and *Euphrasia salisburgensis* subsp. *lapponica*. In the Western Carpathians, a similar vegetation can be seen in the alpine vegetation of the *Oxytropido-Elynion myosuroidis* Br.-Bl. (1948) 1949 alliance in the Belianske Tatry Mts (Šibík et al. 2007), where *T. pumilum* does not occur. In the second, smaller occurrence of *Trichophorum pumilum* in Scandinavia in the mountains in southern Norway, Engelskjøn & Skifte (1987) records this species in fens and fen grasslands scattered in pine and birch woodlands at altitudes between (760) 920 and 980 m a. s. l. This vegetation is again somewhat similar to the *T. pumilum* vegetation of the *Caricion atrofusco-saxatilis* alliance in the Alps, as evidenced by the occurrence of *Carex capillaris*, *C. capitata*, *C. microglochin*, *C. vaginata*, *Juncus arcticus*, *Kobresia simpliciuscula*, *Thalictrum alpinum*, *Selaginella selaginoides* and *Saussuera alpina*. The soil is very mineral-rich and its pH varies between 6.4 and 6.9 (Engelskjøn & Skifte 1987).

Conclusions

In Norway and the Alps, *T. pumilum* occurs predominantly in arctic-alpine vegetation of the *Oxytropido-Elynion myosuroidis* and *Caricion atrofusco-saxatilis* alliances and only rarely in *Caricion davallianae* fens. In the Western Carpathians, *T. pumilum* does not occur in arctic-alpine vegetation and within the *Caricion davallianae* alliance it prefers those types in which there are halophytic species. The reason for this somewhat different ecological behaviour are the specific ecological conditions associated with travertine springs and surrounding fens that enabled the in situ postglacial survival of this species at rather low altitudes in the temperate zone – mean annual temperature 5–7 °C, annual precipitation 500–900 mm (Miklós 2002). In addition, Western-Carpathian populations occur in a region that was not glaciated during the Last Glacial Maximum. Both the stability of the Western-Carpathian travertine habitats during the glacial and postglacial periods and the high salt content resulted in the development of the Western-Carpathian *T. pumilum* habitats, especially those belonging to the *Glauco-Trichophoretum pumili* association, which resemble the continental saline fen grasslands in the Russian Altai Mts, the landscape which is considered to be similar to that which occurred in full-glacial Europe (Horsák et al. 2010). A mixture of (sub)halophytic and calcareous fen species is a common feature of both Western-Carpathian and Central-Asian *T. pumilum* wetlands. In contrast, *T. pumilum* vegetation in the Alps and Norway is a result of a more recent assembly in alpine or arctic zones, in which both calcareous-fen and alpine-tundra species play an important role. In the Western Carpathians, a similar development did not occur because both the prevailing crystalline bedrock and the rugged topography did not support the development of calcareous fen in the alpine zone; many of the fen species that form alpine fens in the Alps occur only in fens below the timberline in the Western Carpathians (Sekulová et al. 2011, 2013). The extreme rarity and specifity are arguments for thorough conservation and monitoring of Western-Carpathian populations of *T. pumilum*.

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Souhrn

Reliktní druh *Trichophorum pumilum* se v rámci svého rozsáhlého, značně disjunktivního areálu vyskytuje v Evropě jen v Alpách, v Norsku a v malém území centrálních Západních Karpat na Slovensku. V příspěvku přinášíme vegetační a ekologické charakteristiky posledních populací druhu v Západních Karpatech a jejich porovnání s ostatními částmi evropského areálu. Na Slovensku je výskyt druhu soustředěný v malém prostoru vnitrokarpatských kotlin (Liptovské, Popradské a Hornádské) a přilehlých úpatích některých pohoří. V současnosti je znám z 10 lokalit na reliktních vápnitých slatinách, vzniklých převážně v pozdním glaciálu v okolí extrémně mineralizovaných pramenů, kde se přímo z vody sráží uhličitan vápenatý. Vyskytuje se ve slatiništních společenstvech (třída *Scheuchzerio palustris-Caricetea nigrae*, svaz *Caricion davallianae*, asociace *Glauco-Trichophoretum pumili* a *Caricetum davallianae*) s výskytem slanomilných druhů rostlin (nejčastěji *Triglochin maritima*). Biotopy a na ně vázaná vegetace se výrazně liší od většiny ostatních evropských lokalit, s výjimkou několika slatin v Alpách, kde však chybějí slanomilné druhy. V Alpách a Norsku se druh *Trichophorum pumilum* vyskytuje prevážně v arkto-alpinské vegetaci svazu *Oxytropido-Elynion* a v slatinné vegetaci svazů *Caricion atrofusco-saxatilis* a *Caricion davallianae*. V západokarpatské arele nebyl druh *T. pumilum* nikdy zaznamenán v arkto-alpinské vegetaci. Důvodem odlišného ekologického chování druhu v Západních Karpatech jsou specifické ekologické podmínky stanovišť ovlivněných minerálními prameny s tvorbou pramenitu (travertinu). Specifické podmínky umožnily přežití druhu in situ během postglaciálu v relativně nízkých nadmořských výškách mírného pásma. Dalším důvodem pravděpodobně je, že západokarpatské populace se vyskytují v oblasti, která nebyla v posledním glaciálním maximu zaledněna. Vysoká stabilita stanovišť extrémně vápnitých slatin vzniklých na minerálních pramenech a velký obsah solí jsou patrně důvodem, proč se západokarpatská stanoviště druhu *T. pumilum* ekologicky podobají kontinentálním slatinám s halofyty v oblasti centrálního ruského Altaje. Krajina centrálního Altaje je považovaná za nejlepší analogii evropské glaciální krajiny. Společný výskyt slanomilných druhů a druhů vápnitých slatin je společným znakem mokřadů s výskytem *T. pumilum* v Západních Karpatech a v centrální Asii. Naopak, vegetace v Alpách a v Norsku představuje spíše (vysoko)horskou vegetaci svazů *Caricon davallianae* a *Caricion atrofusco-saxatilis* v alpínském stupni utvářenou až během Holocénu, ve které vedle typických druhů vápnitých slatin rostou tundrové a vysokohorské druhy. V horách Západních Karpat podobný vývoj neprobíhal, protože převažující krystalické podloží a nevhodné topografické podmínky nedovolily vznik a existenci vápnitých slatin ve vyšších horských polohách. Ojedinělost a mimořádná vzácnost vegetace jsou argumentem pro důslednou ochranu a taktéž další výzkum západokarpatských populací druhu *Trichophorum pumilum*.

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