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Habitat diversity of central European fens in relation to environmental gradients and an effort to standardise fen terminology in ecological studies

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Abstract

Mire terminology, subdivision and gradient structure have been subjected to an intense debate intensified in the last years. The conception of Wheeler and Proctor (J. Ecol. 88, 187–203), which divides mires into bogs, having $\mathrm{pH} < 5.5$, and fens, having $\mathrm{pH} > 5.5$, becomes generally accepted despite a certain critique from the Scandinavian perspective and despite the fact that few contributions to the debate have come from central and southern Europe and from other than botanical disciplines. In this paper, we demonstrated that the bog-fen boundary is clearly determinable not by pH, but by a set of nutrient-requiring species that avoid truly ombrotrophic conditions in central Europe. We therefore defined fens as groundwater-fed wetlands that host low productive nutrient-limited vegetation dominated by Cyperaceae and bryophytes. The fertility gradient within fens, another controversial point in the ongoing debate, is easily distinguishable using both plant and animal data, but it appears primarily within calcium-richer fens. We suggest defining fen grasslands by the high abundance of nutrient-requiring grasses and forbs rather than purely by fen origin and management. Concerning pH/calcium gradient, there is large variation in plant, mollusc, algal, fungal and testacean assemblages within fens with a $\mathrm{pH} > 5.5$ in central Europe even though some authors named all mires having such pH '(rich) fens'. This clear and extended poor–rich (pH/calcium) gradient in floristical data is independent of the fertility gradient. Conductivity (approximating water mineral richness) contributes significantly to the pH in explaining the vegetation variation. Vegetation composition accounts for a larger amount of the variation in algal, molluscan, testacean and fungal assemblages than even long-term measured environmental data. The chemical limit of the occurrence of any *Sphagnum* species, even the calcitolerant ones, is the most important and easily recognised natural boundary between major functional fen types, although it varies among regions and hydrological situations. We therefore believe that fen classification based exclusively on floristic data is necessary to avoid circular argumentation and provides the best basis for the characterization of habitats. We propose to subdivide fens into five standard vegetation types with defined boundaries: poor fens (Sphagno recurvi-Caricion canescentis), moderately rich fens (Caricion fuscae), rich fens (Sphagno warnstorfii-Tomenthypnion), extremely rich fens and calcareous fens (both corresponding to Caricion davallianae). Calcareous fens were neglected during the ongoing debate due to its relative scarcity in some traditionally explored regions. Its ecological boundary is the point at which calcium carbonate starts to precipitate, which is connected with marked change in plant and animal species composition. The ecological differentiation of all proposed fen types was tested using a data set from two different regions (Carpathians and

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Bulgaria). Both conductivity and pH differ significantly between pairs of vegetation types. All proposed fen types also markedly differ in molluscan assemblages.

Keywords: Bog; Conductivity; Molluscs; Mire ecology; pH; Poor–rich gradient; Vegetation

Introduction

The increasing need for rationalisation and standardisation of mire terminology has led to the useful review of Wheeler and Proctor (2000), who proposed the division of mires into two distinct types: bogs having a pH < 5.0 and fens having a pH > 5.5, rather than into minerotrophic fens and ombrotrophic bogs (see also Bridgham et al., 1996). The further division should follow the fertility gradient. The review by Wheeler and Proctor (2000) stimulated an intense debate, which has not died away so far. From the Scandinavian perspective, Økland et al. (2001) argued that a fertility gradient has not been detected in Fennoscandian studies, that the pH bimodality is unclear or inconsistent in many regions, and that the abandonment of traditional division of mires into ombrotrophic and minerotrophic ones would cause extensive confusion. Nakamura et al. (2002) discussed the application of Wheeler and Proctor's terminology for Japanese mires; Sjörs and Gunnarsson (2002) focused on the analysis of water pH and calcium variation in mire waters. Some other recent sound and important papers markedly contribute to this scope (Vitt, 2000; Amon et al., 2002; Tahvanainen and Tuomaala, 2003; Tahvanainen, 2004; Bragazza et al., 2005a). However, few arguments have come from outside the traditionally explored areas in NW Europe and in North America as well as from other biological disciplines that need a clear and unequivocal classification of mire habitats. Little attention has also been paid to the consistency of fen division along the pH/calcium ('poor–rich') gradient. In this review paper we discuss the question of mire subdivision in the light of the current research on biodiversity of various taxonomical groups in central and southern Europe. Special attention will be paid to molluscs—an animal group of extraordinary importance in bioindication of past and present habitat qualities (e.g. Ložek, 1964, 2000; Meyrick and Preece, 2001). The text is structured into the following sections:

1. What is a fen and what is a bog?
2. Fens, fertility and human alternation
3. Fens and the poor–rich gradient
4. Fen classification and pH
5. The standardization of fen type terms
6. Testing the proposed fen types—the case studies
7. Context- and scale-dependence of the poor–rich gradient
8. Conclusions

Nomenclature of plants follows Kubát et al. (2002) for vascular plants and Kučera and Váňa (2003) for bryophytes.

What is a fen and what is a bog?

Some authors replying to Wheeler and Proctor (2000) wished to retain the classical division of mires into ombrotrophic bogs and minerotrophic fens. We agree with the statement of Økland et al. (2001) that the mineral soil water limit is more or less hydrologically distinct and that it is characterised by at least a local set of fen indicator species. Bragazza et al. (2005a) presented a good example of that: minerotrophic habitats have been discontinuously separated from ombrotrophic ones in two single ordinations from Swedish and Italian mire complex. It is true that there seem nowhere to be any bog indicators which do not grow in fens, but on the other hand the nutrient-requiring species occurring commonly in both fens and fen grasslands are fen indicators at the bog-fen boundary in central Europe. The plant species differentiating poor fens from central-European ombrotrophic bogs are, for example, *Viola palustris*, *Agrostis canina, Carex echinata, C. panicea, C. lasiocarpa, C. rostrata, Nardus stricta, Anthoxanthum odoratum, Festuca rubra, Lysimachia vulgaris, Juncus* spp. div. and *Equisetum* spp. div. They benefit from rather high ammonium and phosphate concentrations being found in poor fens (Neuhäusl, 1975; Bertram, 1988; Hájek and Hekera, 2004; Paulissen et al., 2004; Navrátilová et al., 2006). Using the transects from poor fens (lagg) to bogs, Bragazza and Gerdol (2002) and Bragazza et al. (2005a) observed a clear difference in water nitrogen concentrations between poor fens and ombrotrophic bogs. The decline in peat nitrogen content associated with the fen–bog floristic boundary is generally also evident from mire stratigraphy (e.g. Glaser et al., 2004). By analogy, Malmer and Wallén (2005) have found maximum nutrient concentration in plants in moderately-poor fens. Further, a clear distinguishing between minerotrophic and ombrotrophic mires is necessary for recent global ecology studies dealing with field investigations of changes in nutrient limitation caused by increasing atmospheric deposition (e.g. Bragazza et al., 2004, 2005a). Not only nutrient availability, but also water pH differs between fens and bogs. However, this holds primarily for minimum pH rather than for mean values (Asada, 2002). High iron concentration in fens as compared to bogs (Wells, 1996; Hájek et al., 2002) also has a great ecological importance (see Snowden and Wheeler, 1993).

A great ecological difference between ombrotrophic bogs and minerotrophic fens is reflected in both species composition and vegetation structure. In ombrotrophic bogs, complex adaptations of plants are necessary in order to grow there due to extremely low nutrient availability, cold environment, anoxia and toxic influence of hydrogen ions. Only several plant families (e.g. Ericaceae, Vacciniaceae, Sphagnaceae) were able to evolve in this way. The classical division of mires into minerotrophic fens and ombrotrophic bogs is practical also from the zoological point of view. Truly ombrotrophic bogs, composed of extremely acid hummocks and dystrophic hollows and pools, support the existence of few (semi)terrestrial or aquatic invertebrates. On the contrary, several less demanding mollusc species have been found in *Sphagnum*-dominated acidic calcium-poor fens, but always in patches not completely covered by peat mosses (Horsák and Hájek, 2003; Horsák, 2006).

Another point of debate is the differentiation of fens against other freshwater wetlands such as swamps and marshes. Fens have been often defined according to peat depth and/or the percentage of organic matter. Bayley and Mewhort (2004), however, showed that vegetation types of both fen and marsh habitats are capable of having significant peat deposits and that they differ rather in nutrient availability. Kotowski et al. (2006), by analogy, found that a higher nutrient availability promotes a succession from sedge-moss fen communities towards tall-sedge (i.e. marsh) communities. In central Europe, many wetland habitats host exclusively fen species, such as low sedges, cotton grasses and brown mosses, despite low organic matter content and shallow peat layer (Hájek et al., 2002). We therefore decided to define fens as groundwater-fed wetlands that host low productive nutrient-limited vegetation dominated by Cyperaceae and bryophytes.

We should finally note that the term 'fen' has a very narrow sense in many central-European, mostly older vegetation studies. The scientific community, influenced by a German tradition, sometimes distinguishes bogs (ombrotrophic raised mires, 'Hochmoore' in German), transitional mires (minerotrophic *Sphagnum*-fens, 'Übergangsmoore') and fens ('Flachmoore', 'Niedermoore'). The latter term often refers only to strongly calcareous brown-moss fens without any *Sphagnum*. Nevertheless, central-European vegetation science has been gradually abandoning this tripartition.

Fens, fertility and human alternation

Central-European data provide good evidence for a fertility gradient independent of the pH/calcium gradient. Apart from very productive and species-poor reed and tall-sedge vegetation developed in valley fen complexes influenced by polluted river water (e.g. classical locality Biebrza in Poland; see Wassen et al., 1990), the fertility gradient is often connected with an increasing number of nutrient-demanding grassland species in low-productive fen vegetation. The reason why this fertility gradient has not been demonstrated in Fennoscandia is not only a low nutrient supply (Økland et al., 2001), but also a low calcium level in central and norther Fennoscandian mires. In central Europe, the fertility gradient appears primarily at the 'rich' end of the pH/calcium (poor–rich) gradient even in rather unpolluted areas of the Carpathians (Hájek, 2002; Hájek et al., 2002; Hájková et al., 2004) and the Balkans (Hájková et al., unpubl. data). It is probably mediated by a variation in water level dynamics that could also take place under natural conditions. The decrease of the water table causes nutrients to mineralise (Grootjans et al., 1986; Dierßen and Dierßen, 2001) and the topmost soil layer to desiccate in rich fens, but this effect is buffered by a thick layer of live or semidecomposed *Sphagnum* material in poor fens (Hájková et al., 2004). Flintrop (1994) has found that the gradient from rich fens to fen grasslands was connected primarily to summer water table and that additional nitrogen input was not essential for the existence of 'fertile' fen meadows.

Especially the first phase of nutrient enrichment from groundwater or water table decrease is not always connected with strongly increasing productivity, but causes the appearance of grasses and forbs typical of wet Calthion meadows. Van der Hoek et al. (2004), for example, changed the species composition from a fen vegetation dominated by *Carex panicea* to a grassland community with abundant *Holcus lanatus* by a short-time phosphorus fertilisation. Such transitional communities between fens and grasslands are among the species-richest vegetation types of central-European wetlands (Hájková and Hájek, 2003; Hájek et al., 2005). Güsewell et al. (2005) have found that plots with intermediate tissue N:P ratios, i.e. intermediate phosphorus limitation, were on average most species-rich among Swiss, Dutch and American fens or wet grasslands. The increasing nutrient input is not always detectable in soil water (Hájek and Hekera, 2004), but it is reflected by higher tissue concentrations of N, P, K and Ca, especially at the community level

(Z. Rozbrojová, unpubl. data). The terrestrial snails reflect this gradient within fens surprisingly well. The changes of mollusc community composition are mainly caused by different hydrological regime and productivity of grassland habitats. The fen specialists are gradually replaced by ubiquitous species (e.g. *Cochlicopa lubrica*, whose abundance sharply increases) and by shrubland and woodland dwelling ones (e.g. *Fruticicola fruticum*), which start to colonise the site.

For above mentioned reasons we propose to classify fens, among others, according to fertility which is reflected by the representation of nutrient-requiring grassland species. We prefer to define 'fen grasslands', corresponding to Calthion and Molinion alliances in a syntaxonomical classification system, by the high abundance of grassland species such as grasses and forbs rather than purely by fen origin and management. In the western Carpathian flysch zone, spring fen development was in most cases initiated and conditioned by human activities connected with the colonisation of the region, deforestation, grazing and hay making (Rybníčková et al., 2005). Due to phosphorus limitation, the small tufa-forming calcareous fens scattered within a mosaic of managed grasslands very often have species composition identical to natural fens which have not been altered by man. The recent cessation of traditional mowing for hay-making causes the disappearance of fen species and paradoxically it increases the representation of nutrient-requiring grassland species (Diemer et al., 2001; Hájek et al., 2002).

Having now defined fen grasslands as the fens with a high representation of grasses and forbs, we need to cope with a great floristic variation within such defined habitat. The major gradient in floristic variation within wet grasslands is controlled by pH (Blackstock et al., 1998; Hájek and Hájková, 2004) and a great floristic difference exists between mineral-poor and mineral-rich wet grasslands. We therefore propose to divide fen grasslands further, according to the poor–rich gradient, into 'poor fen grasslands', 'rich fen grasslands' and 'calcareous fen grasslands' (Fig. 1). For differences between 'rich' and 'calcareous' see the next Section.

Fens and the poor–rich gradient

Little attention has been devoted to fen classification along the pH/calcium ('poor–rich') gradient during the ongoing debate. Wheeler and Proctor (2000) named all mires having $\mathrm{pH} > 5.5$ '(rich) fens' and did not suggest any further subdivision according to base richness. Nevertheless, there is a large variation in plant (Hájek et al., 2002), mollusc (Horsák and Hájek, 2003), testacean (Opravilová and Hájek, 2006) and algal (Poulíčková et al., 2003) assemblages within fens of $\mathrm{pH} > 5.5$. Økland et al. (2001) suggested a division of the poor–rich gradient into seven habitat types traditionally distinguished in Fennoscandian literature. Sjörs and Gunnarsson (2002) have demonstrated that these fen types correlate only very loosely with water chemistry. By analogy, Nakamura et al. (2002) and Tahvanainen (2004) did not find a tight correlation between calcium concentration and mire vegetation types. On the contrary, calcium and pH were shown to be the major determinants of floristic variation in central-European mires (Rybníček, 1974, Waughmann, 1980; Dierßen and Dierßen, 1984; Flintrop, 1994; Gerdol, 1995; Martinčič, 1995; Hájek et al., 2002; Kutnar and Martinčič, 2003; Hájková and Hájek, 2004a; Navrátilová and Hájek, 2005). Corresponding results are reported from North America (Vitt and Slack, 1984; Vitt and Chee, 1990; Anderson and Davis, 1997; Vitt, 2000; Mullen et al., 2000) and even by some Scandinavian authors (see Malmer, 1986: Fig. 5). How to explain this apparent discrepancy?–Sjörs and Gunnarsson (2002) have used an original, rather fine classification made mostly subjectively by various authors. They related it to the water chemistry data measured at different times and most probably also using differing methods (see Tahvanainen and Tuomaala, 2003). The result they have obtained reflects these methodical constraints. For an exact evaluation of differences in water chemistry between vegetation types, clearly and unequivocally defined vegetation types are needed. Vegetation classifications, however, have often been subjected to criticism. The central and west European phytosociological (syntaxonomical) approach recently copes with the critique about subjectivism and inconsistency by an effort to standardise and formalise the classification process and by efforts towards unifying national classification systems (e.g. Rodwell et al., 1997; Bruelheide and Chytrý, 2000; Kočí et al., 2003; Botta-Dukát et al., 2005). We wish to stimulate an analogical formalisation process in the classification of fen habitats along the poor–rich gradient. This could provide also a good opportunity to join the syntaxonomical classification system with the fen types being traditionally distinguished in NW Europe and N America. Before we will propose anything concerning this standardisation we should shortly address the question what is a real environmental determinant of vegetation variation along the poor–rich gradient. Some recent authors (Nakamura et al., 2002; Tahvanainen, 2004) have reported that pH is a single factor categorising fen types, while the effect of calcium is largely caused by the covariation with pH. Ombrotrophic bogs, poor fens and rich fens can indeed be distinguished solely based on water pH. However, the cited authors have studied a rather wide, nevertheless still incomplete poor–rich gradient. The absence of truly calcium- and carbonate-rich fens is especially conspicuous in C and N

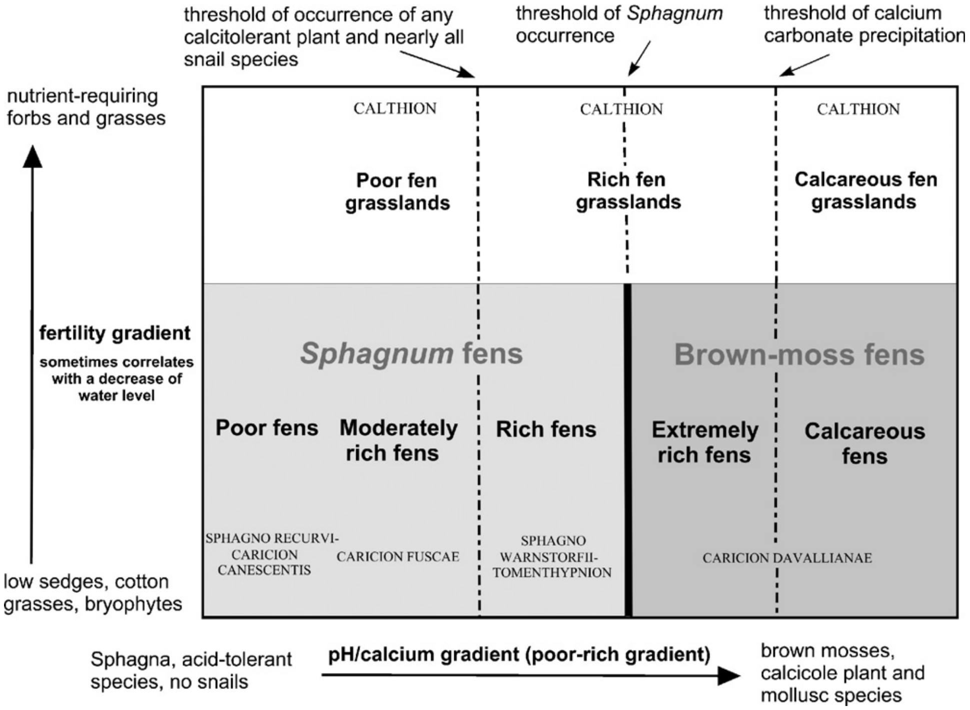

Fig. 1. The relationships between proposed fen types and the poor–rich and fertility gradients, syntaxonomical system and major functional and structural boundaries within fens.

Fennoscandia. The Pleistocene glaciations eroded practically all calcareous material and caused that the majority of groundwater in C and N Fennoscandia is non-calcareous (Tahvanainen, 2004). Vegetation primarily reflects the variation in water pH changing due to accumulation of dissolved organic carbon (Tahvanainen et al., 2002) or due to water aeration (Tahvanainen and Tuomaala, 2003) caused for instance by water flow. The richest Scandinavian fens developed on crystalline bedrock would fall rather within the poor part of the poor–rich gradient on central-European flysch and limestone bedrock (Waughmann, 1980; Hájek et al., 2002). In the westernmost Carpathians and in Bulgaria, we have observed a continuation of plant and animal species turnover along the gradient of increasing calcium concentration in circumneutral and alkaline spring-fed fens (e.g. Horsák and Hájek, 2003, Horsák, 2006, see also Table 1). The role of calcium in this compositional change seems to be clear. The comparison of relatively low calcium concentration in plant tissues and rather high calcium concentration in environment (e.g. Malmer, 1986; Ernst and Nelissen, 1998; Rozbrojová, unpubl. data) shows that plant cells keep superfluous calcium out. Not only hydrogencarbonates (Lamers et al., 1999) but probably also calcium is toxic for *Sphagnum* (cf. Andrus, 1986). Stable high concentrations of both hydrogencarbonates and calcium make the occurrence of even calcitolerant peat mosses impossible. The autogenic succession towards acid habitats is therefore arrested and acidification does not occur even at the fen surface. All even slight acidophytes are absent and a large set of calcicole plant and animal species occurs in strongly calcareous fens, including the species not able to compete with *Sphagnum* for space (Malmer et al., 1994) and the species requiring or tolerating an extraordinary supply of minerals (*Schoenus ferrugineus*, *S. nigricans*, *Sesleria uliginosa*, *Carex hostiana*; e.g. Kopecký, 1960; Tyler, 1979b; Bernhardt, 1994; Hájek and Háberová, 2001). The fungal assemblages also change completely after crossing the chemical limit of calcitolerant peat mosses as the species generally confined to *Sphagnum* substrate (e.g. *Galeriana tibiicystis, Entoloma conferendum, Hygrocybe coccineocrenata*) are replaced by meadow species (e.g. *Coprinus alachnui*) and species populating brown mosses (e.g. *Arrhenia lobata*) (Vašutová, 2005). Moreover, a high calcium concentration causes unavailability of phosphorus and iron, and thus restricts many other plant species (Boyer and Wheeler, 1989; Bedford et al., 1999; Tyler, 2003). The absence of meadow Molinietalia species is reflected by the decrease of species richness in strongly calcareous fens (Chytrý et al., 2003). Precipitated calcium carbonate changes both soil structure and surface temperature. This leads to the occurrence of obligate dryland snail or plant species (Horsák and Hájek, 2003; Hájková et al., 2004) even in fen habitats with only slightly and seasonally decreased water level and, in extreme cases, to subhalophytic conditions that do not support occurrence of many invertebrates (Horsák, 2006). In addition, when we include calcareous fens in the study

Table 1. Vegetation table with fidelity values showing the differences between the proposed five fen types in the western Carpathians

Fen type	CF	ERF	RF	MRF	PF
Number of plots	184	87	119	51	69
Calcareous fens					
Palustriella commutata	**52.9**	6.0	—	—	—
Carex flacca	**50.8**	—	—	—	—
Primula farinosa	**44.8**	—	9.5	—	—
Parnassia palustris	**44.4**	1.5	10.3	—	—
Carex lepidocarpa	**43.9**	—	0.9	—	—
Triglochin maritima	**41.5**	—	—	—	—
Triglochin palustre	**40.7**	13.3	5.6	—	—
Valeriana dioica	**39.0**	—	—	—	—
Carex distans	**36.7**	—	—	—	—
Carex davalliana	**34.8**	9.5	16.7	—	—
Pinguicula vulgaris	**34.0**	—	16.1	—	—
Juncus articulatus	**33.6**	17.4	9.6	—	—
Carex hostiana	**28.8**	—	3.5	—	—
Philonotis calcarea	**28.6**	4.5	—	—	—
Blysmus compressus	**26.0**	10.7	—	—	—
Fissidens adianthoides	**25.8**	5.4	15.3	—	—
Tofieldia calyculata	**25.3**	—	5.0	—	—
Dactylorhiza incarnata	**25.1**	—	—	—	—
Gymnadenia densiflora	**24.1**	12.3	—	—	—
Carex paniculata	**23.8**	—	2.9	—	—
Taraxacum Sect. *Palustria*	**23.1**	2.1	—	—	—
Salix rosmarinifolia	**22.3**	—	3.8	—	—
Trichophorum pumilum	**22.0**	—	—	—	—
Schoenus ferrugineus	**22.0**	—	—	—	—
Eleocharis quinqueflora	**20.2**	17.4	8.7	—	—
Calcareous and extremely rich fen					
Eriophorum latifolium	**33.6**	**38.6**	11.8	—	—
Bryum pseudotriquetrum	**30.8**	**33.8**	17.3	—	—
Epipactis palustris	**30.1**	**23.0**	—	—	—
Scorpidium cossonii	**27.7**	**26.5**	16.9	—	—
Calliergonella cuspidata	**23.8**	**22.1**	13.7	—	—
Cirsium rivulare	**20.4**	**25.3**	—	—	—
Campylium stellatum	**39.6**	**29.4**	**20.4**	—	—
Extremely rich fens					
Valeriana simplicifolia	4.6	**36.5**	9.7	—	—
Linum catharticum	3.2	**36.3**	2.5	—	—
Plagiomnium elatum	18.8	**35.7**	8.3	—	—
Equisetum palustre	16.5	**30.1**	7.0	—	—
Dactylorhiza majalis	4.3	**29.7**	8.4	—	—
Crepis paludosa	—	**21.2**	17.2	—	—
Equisetum variegatum	11.3	**20.1**	—	—	—
Hamatocaulis vernicosus	—	**20.0**	16.8	—	—
Extremely rich and rich fens					
Carex panicea	15.6	**22.8**	**23.6**	—	—
Galium uliginosum	—	**20.3**	**24.6**	—	—
Rich fens					
Sphagnum warnstorfii	—	—	**62.6**	—	—
Sphagnum teres	—	—	**39.5**	10.7	—
Sphagnum contortum	—	—	**39.4**	7.1	—
Aulacomnium palustre	—	6.7	**39.3**	1.1	—
Homalothecium nitens	0.3	16.7	**31.8**	—	—

Table 1. (*continued*)

Fen type	CF	ERF	RF	MRF	PF
Carex dioica	—	3.3	**29.9**	—	—
Carex chordorrhiza	—	5.0	**25.0**	—	—
Carex flava	0.7	13.9	**23.4**	—	—
Paludella squarrosa	—	—	**22.1**	3.4	—
Carex pulicaris	—	0.5	**21.6**	—	—
Hypnum pratense	—	9.0	**20.6**	—	—
Chiloscyphus polyanthos	—	—	**20.2**	—	—
Rich and poor fens					
Drosera rotundifolia	—	**—**	**25.2**	4.2	**22.4**
Moderately rich fens					
Sphagnum subsecundum	—	—	1.0	**31.7**	—
Straminergon stramineum	—	—	9.4	**26.5**	9.8
Ranunculus flammula	—	—	—	**26.4**	—
Philonotis seriata	—	—	—	**25.2**	—
Juncus filiformis	—	—	—	**22.8**	2.5
Warnstorfia exannulata	—	—	2.1	**22.3**	4.8
Warnstorfia sarmentosa	—	—	—	**22.3**	—
Moderately rich and poor fens					
Viola palustris	—	—	2.5	**22.7**	**25.5**
Nardus stricta	—	—	—	**20.7**	**26.6**
Poor fens					
Sphagnum fallax	—	—	—	**1.6**	**60.4**
Polytrichum commune	—	—	—	**—**	**57.2**
Oxycoccus palustris	—	—	15.3	**—**	**36.6**
Sphagnum palustre	—	—	—	**3.4**	**36.3**
Sphagnum magellanicum	—	—	—	—	**36.0**
Sphagnum flexuosum	—	—	8.5	3.7	**29.8**
Sphagnum papillosum	—	—	—	—	**26.6**
Sphagnum capillifolium	—	—	4.0	4.5	**26.6**
Carex canescens	—	—	—	15.5	**25.7**
Eriophorum vaginatum	—	—	—	16.4	**25.3**
Sphagnum rubellum	—	—	—	—	**22.3**

Vegetation plots were classified according to floristic criteria. The table shows only the species that reach high fidelity to some of the fen vegetation types. Fidelity was calculated as *phi*-coefficient (Chytrý et al., 2002a,b), the threshold value for inclusion to the table was arbitrarily set at 20. The species with a clear optimum outside fen vegetation are shown only below the table. The species groups that were used in habitat classification are presented at the end of the table (for details of classification see the text).

CF = calcareous fens; ERF = extremely rich fens; RF = rich fens; MRF = moderately rich fens; PF = poor fens.

Species with a clear optimum outside fens:

CF: *Juncus inflexus* 46.9, *Eupatorium cannabinum* 45.8, *Tussilago farfara* 32.2, *Mentha longifolia* 29.2; *Cratoneuron filicinum* 28.5, *Sanguisorba officinalis* 26.0, *Agrostis stolonifera* 25.3, *Hypericum tetrapterum* 24.9, *Lysimachia nummularia* 24.9, *Schoenoplectus tabernaemontani* 24.9, *Molinia caerulea* agg. 24.0, *Carex tomentosa* 23.0, *Galium verum* 21.3, *Cirsium canum* 21.0, *Potentilla reptans* 21.0, *Lythrum salicaria* 20.7, *Chara* spp.div. 20.7, *Carex hirta* 20.6, *Bromus erectus* 20.3

ERF: Climacium dendroides 34.1, Prunella vulgaris 32.6, Lathyrus pratensis 30.9, Cruciata glabra 27.3, Ranunculus acris 26.4, Alchemilla vulgaris agg. 25.1, Briza media 25.0, *Leontodon hispidus* 22.7, *Lychnis flos-cuculi* 21.4, *Vicia cracca* 20.9, *Trifolium pratense* 20.4, *Luzula multiflora* 24.6

RF: *Filipendula ulmaria* 22.5, *Succisa pratensis* 21.2

MRF: *Ligusticum mutellina* 21.8; *Atrichum undulatum* 21.7; *Lycopus europaeus* 20.4

PF: *Calamagrostis canescens* 34.1, *Melampyrum pratense* 32.1, *Avenella flexuosa* 28.8, *Calamagrostis villosa* 21.3

Species groups that were used in habitat classification:

Group of calcicole species (*Carex davalliana* group): *Carex davalliana, C. lepidocarpa, Scorpidium cossonii, Eriophorum latifolium, Parnassia palustris, Primula farinosa, Pinquicula vulgaris, Eleocharis quinqueflora, Triglochin palustre, Campylium stellatum*

Group of *Palustriella* spring fens (*Palustriella commutata group*): *Palustriella commutata, Carex flacca, Eupatorium cannabinum, Juncus inflexus, Tussilago farfara*

Group of acid fens (*Polytrichum commune* group): *Polytrichum commune, Sphagnum fallax, S. magellanicum, S. palustre, S. papillosum*

Group of salt-rich fens (*Trichophorum pumilum* group): *Trichophorum pumilum, Plantago maritima, Glaux maritima, Triglochin maritima, Schoenoplectus tabernaemontanii, Centaurium littorale, Campyladelphus elodes, Carex distans.*

of mineral richness gradient in mires, the often-reported correlation between pH and total mineral richness becomes weaker. Within extremely calcium-rich habitats such as tufa-forming calcareous fens, pH does not correlate significantly with measured mineral concentrations or such correlation can be even negative (Johnson and Steingraeber, 2003; Horsák, 2006). In conclusion, such a different habitat type as strongly calcareous fen should be distinguished carefully from (mostly boreal) fens that have brown-moss dominated vegetation and circumneutral pH, but otherwise low calcium content and no carbonate substrates accumulated (see also Amon et al., 2002).

Fen classification and pH

The next point of debate, to which we would like to contribute, concerns the direct use of environmental data in mire vegetation classification. The characteristics of vegetation types should be solely based on species composition and community structure to avoid circular argumentation in further testing the environmental differences and in arguing for the existence of distinct vegetation types determined by environmental variation. However, do we really need a fen classification based on species data variation along the poor–rich gradient? During our multidisciplinary investigation of western Carpathian mires we have tested whether vegetation composition or directly measured water chemistry data are a better determinant of variation in species composition of mollusc, algal, fungal and testacean assemblages along the poor–rich gradient. In all cases vegetation variation as expressed by DCA site scores accounted for a larger amount of the variation than even long-term measured environmental data (Horsák and Hájek, 2003; Poulíčková et al., 2004; Vašutová, 2005; Opravilová and Hájek, 2006). By analogy, bryophytes were more closely related to the species composition of the vascular plants than to the measured water chemistry (Hájková and Hájek, 2004a; ter Braak and Schaffers, 2004). This implies that fen types based on vegetation composition are necessary for a correct characterisation of fen habitats. The vegetation reflects a long-term development of environmental conditions including hardly measurable ones in the field and including also possible antagonistic or synergistic influences of environmental factors on the fen biota. Another reason why we need fen classification based solely on vegetation data is the fact that no coherent chemical conditions associated with communities exist on the large geographical scale (Wheeler, 1999). This is largely due to different water sampling methods and sampling times applied by each author (see Tahvanainen and Tuomaala, 2003; Hájek and Hekera, 2004), but also by the synergistic influence of some water chemistry variables. This trait can especially alter the chemical limits of rich fens with respect to poor fens. In central Europe some fen waters are extraordinary rich in iron or phosphates. Both elements can decrease the intolerance of some *Sphagnum* species to high calcium levels. Iron, at least partly, substitutes for calcium at the cation exchange sites in *Sphagnum* (Andrus, 1986) and this can cause the iron-tolerant species *S. flexuosum* and *S. subsecundum* to dominate in rather calcium-rich fens (Prát, 1960; Hájek et al., 2002; Hájková, 2005). Phosphorus and ammonium availability was by analogy revealed to have crucial impact on *Sphagnum fallax* populating the mineral-rich fens (Kooijman and Kanne, 1993; Paulissen et al., 2004; Navrátilová et al., 2006). The dominance of these peat mosses is soon afterwards mirrored by a steep decrease in pH and by a rapid change from a rich to a poor fen; with all consequences for invertebrate assemblages. We further hypothetise that water flow is the next factor which can shift the chemical limit of a given fen vegetation type. The continuous supply of even a small amount of calcium in high-pH, iron-poor and infertile spring water maintains uninterrupted calcium exchange on *Sphagnum* cell walls and can therefore result in the same detrimental level of toxic calcium in *Sphagnum* tissues as in more calcareous but stagnant water acidified by dissolved organic carbon.

Finally, some results from south-European mires represent the next argument for rejecting the fen classification based solely on pH-classes. Muñoz et al. (2003) have repeatedly found a pH range from 5.0 to 7.2 (!) in an extremely calcium-poor fen (below ca 1.5 mg/l) whose vegetation corresponded to typical poor fens (*Sphagnum denticulatum*, *S. flexuosum*, *S. papillosum*, *S. russowii*). This happened due to the measurements of surface water being influenced by an intense algal phytosynthesis in the warm summer.

In this discussion we would like to propose such a basic subdivision of fens along the poor–rich gradient that reflects clear vegetational attributes. We will try to propose a classification which (a) will respect the tradition in mire ecology and therefore will not cause future confusion, (b) will reflect variation in both plant and animal assemblages, (c) will be transferable between particular European regions and (d) will not stay in opposite to syntaxonomical system. The last point, however, supposes some moderate modifications of the European syntaxonomical system.

The standardization of fen type terms

The most commonly used English names of mire vegetation types are as follows (numbers of references in current scientific literature found in Scopus database in October 2005 are in brackets): ombrotrophic bog(s)

(159), poor fen(s) (140), rich fen(s) (190) and calcareous fen(s) (61). Rich fen subdivision into moderate(ly)-rich (22) and extreme(ly)-rich (16) is more often applied than the subdivision of poor fens into extreme(ly)-poor (5) and moderate(ly)-poor ones (3). The term intermediate fen(s) (16) is also marginally used in the current scientific literature. This corresponds to an equivocal conception of moderately-poor and intermediate fens. Both these types displayed an extraordinary large variation with respect to pH (approximately 4.8–7.2) and calcium (approximately 0.5–10 mg/l) in the synthesis of Sjörs and Gunnarsson (2002) based on originally classified data. We therefore propose to abandon the subdivision of poor fens and, on the other hand, to distinguish clearly differentiated calcareous tufa-forming fens from extremely rich in terms of floristic composition, but non-calcareous ones (see above). Further, we would like to propose standard boundaries between the fen types. We believe that following five fen types could be doubtless distinguished along the poor–rich gradient (see also Fig. 1):

1. Poor (*Sphagnum*-) fens (Sphagno recurvi-Caricion canescentis)
2. Moderately rich (*Sphagnum*-) fens (Caricion fuscae)
3. Rich (*Sphagnum*-) fens (Sphagno warnstorfii-Tomenthypnion)
4. Extremely rich fens (Caricion davallianae, only peat-forming communities)
5. Calcareous (tufa-forming) fens (Caricion davallianae, communities forming at least patches of $CaCO_3$ tufa)

The phytosociological alliances that overlap between several of these types or that are strongly ambiguous with respect to their conception are omitted here and might be abandoned after a thorough synthesis of European mire vegetation. This holds especially for Caricion lasiocarpae and Rhynchosporion albae.

Poor (*Sphagnum*-) fens

This type represents prevailingly rather species-poor minerotrophic mires strongly dominated by *Sphagnum* species. In central Europe, *S.* sect. *Cuspidata* (mostly *S. recurvum* group), *S. denticulatum* and *S. papillosum* dominate in waterlogged microhabitats and other *Sphagnum* sect. *Palustria* species, *S. capillifolium* as well as *Polytrichum commune* can dominate in small hummocks. Other non-sphagnaceous mosses are rare and represented only by few interspersed species such as *Straminergon stramineum, Warnstorfia exannulata* and *W. fluitans*. Desmids are the characteristic component of the algal assemblages (Kitner et al., 2004). The vascular plant community is largely different from that of ombrotrophic bogs in central Europe (see Section 'what is a fen and what is a bog?'). The large set of poor-fen bryophytes (e.g. *Sphagnum flexuosum*, *S.* sect. *Subsecunda, Straminergon stramineum, Warnstorfia exannulata, Polytrichum commune*) practically does not enter the unpolluted ombrotrophic bogs in central Europe. The species from *S. recurvum* group reach the extremely high values of biomass production in poor fens, several times exceeding the production of bog peat mosses (Kooijman and Kanne, 1993; Hájková and Hájek, 2003). Only one bivalve, *Pisidium casertanum*, is able to dwell in such calcium-poorest fens (Horsák and Hájek, 2003).

Moderately rich (*Sphagnum*-) fens

The boundary of moderately rich fens towards poor fens is not as sharp as that between poor fens and bogs. It is indicated by an increase in species richness and by the dominance of *Sphagnum* sect. *Subsecunda* or *S. teres* instead of *S.* sect. *Cuspidata*. The moss layer is species-richer and contains for example *S. subsecundum*, *S. subnitens* and *S. teres*, *Straminergon stramineum*, *Warnstorfia exannulata*, *Aulacomnium palustre* and others. The species from the *Sphagnum recurvum* group still occur in this type but they do not produce so much biomass. The calcicole fen species (Table 1) are absent, especially in the vascular plant layer. In central Europe, this habitat type develops largely on young fens with a shallow peat profile or at fishpond and lake margins (Navrátilová & Navrátil, 2005). The high representation of meadow grasses and forbs causes the resemblance to Calthion meadows. This vegetation type is rare in some regions. The relative rarity of moderately rich vegetation and relative low number of habitat specialists is probably due to chemical instability of the intermediate pH of 4.5–6.5 (Gorham and Janssens, 1992; Vitt et al., 1995; Sjörs and Gunnarsson, 2002; Tahvanainen and Tuomaala, 2003). Moderately rich fens are clearly different from poor fens also from the malacological point of view. Not only further freshwater molluscs, but even some land snails start to appear. Nevertheless, the terrestrial malacofauna is species-poor and composed of species with low demand for calcium (e.g. *Vertigo substriata*, *Perpolita hammonis*) (Table 2).

Rich (*Sphagnum*-) fens

In this vegetation type, the calcitolerant peat mosses *Sphagnum teres*, *S. warnstorfii*, *S. contortum* and *S. subnitens* coexist with basicole and calcicole species (e.g. *Eriophorum latifolium*, *Parnassia palustris*, *Epipactis palustris*, *Carex davalliana*) due to habitat quality, i.e. water chemistry representing the niche margins of both calcitolerant peat mosses and extremely-rich-fen species. This results in high species

Table 2. Mollusc table in fidelity values showing differences between proposed fen types in the Western Carpathians

Fen type	CF	ERF	RF	MRF	PF
No. of relevé	81	25	21	5	5
Calcareous fens					
Bythinella austriaca	**48.9**	19.2	—	—	—
Vallonia costata	**48.1**	—	—	—	—
Aegopinella pura	**44.1**	8.3	—	—	—
Succinella oblonga	**44.1**	—	—	—	—
Daudebardia rufa	**43.1**	0.4	—	—	—
Pupilla alpicola	**40.0**	—	—	—	—
Monachoides incarnatus	**39.8**	10.7	—	—	—
Plicuteria lubomirskii	**39.4**	1.9	—	—	—
Acanthinula aculeata	**39.2**	—	—	—	—
Columella edentula	**35.5**	8.6	2.0	—	—
Platyla polita	**34.6**	—	—	—	—
Arianta arbustorum	**33.4**	—	—	—	—
Vertigo moulinsiana	**33.4**	—	—	—	—
Vitrea diaphana	**32.5**	4.7	—	—	—
Pupilla muscorum	**28.4**	—	—	—	—
Alinda biplicata	**26.5**	—	—	—	—
Perforatella bidentata	**25.9**	12.3	—	—	—
Fruticicola fruticum	**23.6**	2.9	—	—	—
Calcareous and extremely rich fens					
Punctum pygmaeum	**52.6**	**32.8**	—	—	—
Vertigo angustior	**51.1**	**27.9**	—	—	—
Oxyloma elegans	**47.4**	**26.1**	—	—	—
Euconulus fulvus	**46.0**	**20.1**	—	—	—
Carychium minimum	**42.0**	**30.9**	13.5	—	—
Vertigo antivertigo	**33.5**	**30.4**	—	—	—
Carychium tridentatum	**33.5**	**25.5**	4.9		
Cochlicopa lubrica	**47.6**	**50.8**	—	—	—
Vallonia pulchella	**47.4**	**50.1**	—	—	—
Vertigo pygmaea	**44.8**	**46.3**	—	—	—
Vitrina pellucida	**24.4**	**33.6**	—	—	—
Extremely rich fens					
Euconulus praticola	16.5	**37.8**	—	—	—
Anisus leucostoma	—	**31.6**	11.4	—	—
Pisidium obtusale	6.5	**26.8**	—	—	—
Zonitoides nitidus	17.2	**24.1**	—	—	—
Deroceras laeve	—	**23.8**	15.4	—	—
Vertigo geyeri	—	**23.6**	18.9	—	—
Rich fens					
Vertigo substriata	2.4	14.5	**22.0**	10.5	—
Moderately rich fens					
Pisidium casertanum	—	10.7	1.8	**29.1**	—

Plots were classified according to floristic criteria (for details of classification see the text). The table shows only the species that reach high fidelity to some of the fen vegetation types. Fidelity was calculated as *phi*-coefficient (Chytrý et al., 2002a, b), the threshold value for inclusion to the table was arbitrarily set at 20.

CF = calcareous fens; ERF = extremely rich fens; RF = rich fens; MRF = moderately rich fens; PF = poor fens.

richness. The superficial structure of this habitat is not so marked like in aapa or mixed mires (see Bellamy and Rieley, 1967; Karlin and Bliss, 1984; Hájková and Hájek, 2004b) and the vegetation makes mostly an impression of rather high homogeneity. The chemical parameters of groundwater can be the same as in the successionally young stages of the following vegetation type, that is extremely rich fens, but the activity of calcitolerant Sphagnum species causes lower pH and lower Ca concentration in surface water (Glime et al., 1982; Kuhry et al., 1993; Tahvanainen and Tuomaala, 2003; Hájková and Hájek, 2004a) and a consequent occurrence of shallow-rooting acidophytes. This vegetation type can develop on crystalline non-calcareous bedrock (Rybníček, 1974) as well as on calcareous flysch or limestone due to autogenic succession. Hájek (1999) has observed that the extremely rich fens lacking *Sphagnum* species, recorded by Pawłowski et al. (1960) in the Polish Carpathians, change gradually into rich *Sphagnum*-fens. During this process, shallow-rooting acidophytes, calcitolerant *Sphagna* and slightly acidophilous bryophytes appear, whereas the set of calcicole vascular plant species remains unchanged.

Some central-European vegetation scientists tend to join rich fens, extremely rich fens and calcareous fens to one vegetation unit (Caricion davallianae s.lat.) due to a similar vascular plant layer dominated most often by *Carex davalliana*. The terrestrial snails, however, seem to have a finer resolution and reflect the different surface-water chemistry and structure of the bottom vegetational layer more precisely (Horsák and Hájek, 2003). The extremely-rich-fen species of snails (e.g. *Vertigo angustior*, *V. pygmaea*, *Vallonia pulchella*) are totally absent in rich *Sphagnum*-fens (Table 2). Only few calcium-demanding snails, such as *Vertigo geyeri*, can tolerate the lower pH and lower mineral level of surface water and form numerous populations in brown-moss patches of rich fens. This trait is presumably connected to the boreal distribution of the species as the poor–rich gradient only scarcely goes behind rich fens in the boreal zone of Europe.

The marked ecological difference between rich *Sphagnum*-fens and extremely rich (or calcareous) fens within too widely drafted ‘rich fens’ (Caricion davallianae) is easy to demonstrate. Dierßen and Dierßen (1984), for example, present a graph showing that a rich fen dominated by *S. warnstorfii* had permanently lower pH not overlapping with the high values of extremely rich fens without *Sphagnum* in spite of *Carex davalliana* dominance in both types.

We can conclude that rich fens are clearly delimited by the occurrence of calcitolerant peat mosses and basiphytes at the one end and by the general limit of *Sphagnum* occurrence at the opposite end. Nevertheless, the concrete values of this chemical limit of *Sphagnum* occurrence can vary between regions and sites dependently on the rate of water flow, water fertility and iron-richness (see above).

Extremely rich fens (peat-forming)

We propose that only fens without *Sphagnum* species are called ‘extremely rich fens’. There seems to be a clear functional and structural boundary mirroring itself in the floristic and faunistic composition of the fen. The organisms associated with *Sphagnum* are absent, e.g. many testate amoebae (e.g. Booth, 2001; Lamentowicz and Mitchell, 2005) and macrofungi (Vašutová, 2005), and only slight superficial acidification caused by decomposition (Vitt, 2000) or by acidification ability of brown mosses (Růžička, 1961; Glime et al., 1982) takes place. The bottom vegetational layer is most typically formed by *Drepanocladus cossonii*, which is accompanied by the other brown mosses dependently on water regime (e.g. *Calliergon giganteum*, *Scorpidium scorpioides*, *Campylium stellatum*, *Bryum pseudotriquetrum*, *Fissidens adianthoides*). *Tomenthypnum nitens* can form hummocks, but without any *Sphagnum* species. All these brown-moss species cannot be, however, regarded as indicators of extremely rich fens (see Scandinavian indicator-species classification, e.g. Sjörs et al., 1999) since they coexist with calcitolerant peat mosses already in the previous vegetation type. Extremely rich fens represent the real threshold for the appearance of rich land-snail communities (Table 2). Many snails start here their occurrence in fens and compose species-rich and very abundant communities. All of them also live in the next type but some of them have their optima here (e.g. *Vertigo geyeri*, *Euconulus praticola*).

This vegetation type involves communities developed in deep and old peat deposits with a stable water regime that are dominated by *Carex lasiocarpa*, *C. chordorrhiza* or *C. diandra* and brown mosses, mostly Amblystegiaceae (Rybníček, 1985; Martinčič, 1995; Gerdol and Tomaselli, 1997; Hájek and Háberová, 2001) as well as those developed in fens with a shallow peat layer whose development was initiated and conditioned by human agriculture activities (Pawlowski et al., 1960; Balátová-Tuláčková, 1974; Hájek and Hájková, 2002). The extremely rich fens are especially endangered ecosystems in many regions, especially in those influenced substantially by man. This is due to an increasing nutrient supply causing a resistance of *Sphagnum* species to high mineral levels (Kooijman and Kanne, 1993) and due to a water level decrease weakening the influence of hydrogencarbonates supplied from groundwater (van Diggelen et al., 1996). *Sphagnum* species can appear in such cases and shift the succession towards rich and poor fens as was confirmed by macrofossils analyses from central Europe (e.g. Rybníček and Rybníčková, 1968), Scandinavia (e.g. Mörnsjö, 1969) and northern America (e.g. Kuhry et al., 1993). In central Europe, the enhanced supply of nutrients to the mires contributes together with the drop of water table to the acceleration of succession towards rich *Sphagnum*-fens and fen meadows. In some cases of moderate nutrient enrichment and simultaneous drop of the water table the natural rich fens advance into a specific more or less stable stage with a bottom vegetational layer composed of calcitolerant peat mosses and a herb layer composed only of ubiquitous grassland species. These changes lead to a dramatic decrease of mollusc species richness as the majority of demanding species disappears.

Calcareous tufa-forming fens

We would like to argue for the distinguishing of calcareous fens—a distinct and conspicuous fen habitat type which has been neglected by both Wheeler and Proctor (2000) and Økland et al. (2001). The ecological boundary between extremely rich fens and calcareous fens is the point at which calcium carbonate starts to precipitate and forms a persisting consolidated tufa or unconsolidated marl (see Amon et al., 2002) at least in small, scattered patches. It is connected to a marked change in the plant and animal species composition. The calcareous fens, mostly classified as the Caricetum davallianae s.s., Schoenetum ferruginei, Schoenetum nigricantis and Carici flavae-Cratoneuretum associations in the syntaxonomical system, are a typical component of European as well as North-American landscapes. They differ substantially even from extremely rich peat-forming fens. The calcium concentration reached up to 322 mg/l in the fens studied in the western Carpathian flysch zone (Hájek et al., 2002), similar maximum values are reported from temperate North America (Amon et al., 2002). No (at least slight) acidophytes, no meadow grasses and few forbs survive in these extremely calcium-rich and extremely nutrient-limited habitats. The number of generalist species increases after the addition of nutrients (Pauli et al., 2002). Phosphorus is generally the limiting nutrient in rich fens, but its available form is even rarer in tufa-forming calcareous fens because high calcium concentration tends to precipitate phosphorus into forms unavailable to plants (Boyer and Wheeler, 1989; Boeye et al., 1997; Bedford et al., 1999). The tissue P concentration of calcareous spring vegetation is substantially lower than that of extremely rich but peat-forming fens (Z. Rozbrojová, unpubl. data).

Drepanocladus cossonii still dominates in peat-forming patches and circumneutral pools, but it is replaced by *Palustriella commutata* and *Philonotis calcarea* at the petrifying patches. *Campylium elodes* and *C. stellatum* have been found to be dominating mosses in Bulgarian *Schoenus nigricans*-fens. The brown moss *Palustriella commutata* is a common dominant and one of the best indicators of calcareous fens. This typically calcicole species is replaced by *P. falcata* in extremely rich, although non-calcareous, fens of Fennoscandia and European high mountains (Hedenäs and Kooijman, 2004). The distribution range of *P. commutata*, avoiding C and N Fennoscandia but involving S Sweden, fits to the distribution range of other species typical of calcareous fens as *Carex hostiana*, *C. lepidocarpa*, *C. davalliana*, *Schoenus ferrugineus*, *S. nigricans*, *Juncus subnodulosus*, *Sesleria uliginosa* and others. American authors (Almendinger and Leete, 1998; Amon et al., 2002) also note that accumulations of precipitated minerals are associated with distribution of certain plant species. On the other hand, slight-acidity indicators as *Aulacomnium palustre*, *Agrostis canina*, *Carex echinata* and *Hypnum pratense* should be absent in calcareous tufa-forming fens.

In some cases, the entire surface of calcareous fen can be covered by the precipitated tufa. The snail fauna is extraordinarily rich; the richest sites host more than 30 species. The easily available calcium causes the malacofauna composition to be a diverse mixture of different ecological groups of molluscs. In western Carpathian fens, more than ten mollusc species (e.g. *Vertigo moulinsiana*, *Pupilla alpicola*) were found only in calcareous tufa-forming fens (Horsák and Hájek, 2003); others have their clear optimum here (e.g. *Oxyloma elegans*). The diatom flora is also very rich and diatom epiphytes on moss plants are very abundant (Poulíčková et al., 2003). The fructifying macro-fungi are nearly completely absent (Vašutová, 2005). All these characteristics are due to tufa (travertine, calcite, chalk, marl) precipitation. As in some previous cases, no coherent chemical limit can be determined between calcareous and extremely rich fens. The tufa precipitation depends not only on the calcium concentration, but also on the rainfall regime, air temperature, water HCO_3^- content, hydrology and iron concentration. It can change even in a single fen in time (Almendinger and Leete, 1998; Hájek et al., 2002; Grootjans et al., 2005).

Calcareous fens are, however, not entirely homogeneous and the large species pool of calcicoles (see Chytrý et al., 2003) provides a great number of classification characters for further divisions. They are easy to subdivide according to local hydrological and biogeographical conditions. We have distinguished three major types of calcareous fens in the western Carpathians, for example. The outer-Carpathian spring-fed fens are strongly tufaceous, small and rather young with respect to postglacial development. The inner-Carpathian fens are larger, older and contain more peat-forming patches (Grootjans et al., 2005). The floristic and faunistic differences between these two biogeographical entities are significant. The third differing habitat type, travertine swards, represents such an extremely mineral- and sulphate-rich habitat that even most calcium-demanding snails are no longer able to live there (Horsák, 2006). The vegetation is characterised by at least slight halophytes (*Glaux maritima*, *Plantago maritima*, *Trichophorum pumilum*, *Schoenoplectus tabernaemontanii*, *Centaurium littorale*) coexisting with other rich-fen species (Vicherek, 1973). Analogous vegetation types are reported from Sweden (Tyler, 1979a), North America (Cooper, 1995) and Siberia (König and Rilke, 2004).

Testing the proposed fen types—the case studies

In order to test both the applicability of the proposed fen classification and the environmental differences among them, we collected 510 lists of plant species with estimated percentage cover in plots of 16–25 m^2 from western Carpathian fens as well as the relevant water pH and conductivity data measured directly in field (for details see Hájek et al., 2002; Hájek and Hekera, 2004; Hájková and Hájek, 2004a). All data were collected during 2001–2005. Water conductivity represents the approximation of total water mineral concentration and in a large extend it correlates with Ca + Mg concentration, especially in calcareous waters (e.g. Hájek et al., 2005). Several species groups were created by the Cocktail method (Bruelheide, 2000; see bottom of Table 1). The vegetation was classified into the five fen types proposed above in the following manner.

Poor fens: vegetation plots dominated by *Sphagnum* sect. *Cuspidata, Sphagnum* sect. *Palustria, S. capillifolium* or characterised by the presence of the *Polytrichum commune* group (Table 1).

Moderately-rich *Sphagnum* fens: vegetation plots without any species from the group of calcicole fen species (Table 1) and not meeting conditions mentioned above.

Rich fens: vegetation plots with a presence of any *Sphagnum* species (they are mostly calcitolerant ones) and with a presence of at least one species from the group of calcicole fen species (Table 1).

Extremely rich fens: vegetation plots without any *Sphagnum* species, with a presence of at least one species from the group of calcicole fen species (Table 1) and not meeting conditions mentioned below (calcareous fens)

Calcareous fens: vegetation plots without any *Sphagnum* species, with a presence of many species from the group of true rich fen species. Simultaneously, at least one species from the species group of salt-rich fens (*Trichophorum pumilum* group, see bottom of Table 1) or from the group of *Palustriella commutata* spring fens (Table 1) must be present or vegetation must be dominated by *Palustriella commutata* or *Carex hostiana* (more than 5% of cover).

The resulting classification (Table 1) was confronted with measured environmental data (Fig. 2). The absolute ranges of pH and conductivity overlapped, but the interquartile ranges were mostly specific for individual vegetation types (Fig. 2). One-way ANOVA revealed slightly greater differences in log-transformed conductivity values ($F = 334.5$, $p < 0.001$) than in pH values ($F = 305.1$, $p < 0.001$) between vegetation types. The Tukey post-hoc test confirmed the hypothesis that both water chemistry variables (pH, conductivity) differ between all pairs of vegetation types (Fig. 2). Both pH and conductivity gradually decreased from calcareous, tufa-forming fens to poor fens. When we consider (1) not entirely consistent environmental data sampling conducted within several years; (2) biases caused by seasonal variation (Hájek and Hekera, 2004); water level fluctuation (Baumann, 1996; Hájková et al., 2004), different weather course in particular years (the warm and dry summer 2004); and (3) the impossibility to keep on absolutely identical sampling procedure in such an extensive study (see Tahvanainen and Tuomaala, 2003), we can regard the robustness of the result to be great. The obtained result was further tested using another independent data set from a different biogeographical region of Bulgaria. The results from the western Carpathians were confirmed. All pairs of vegetation types differed significantly, with an exception of statistically insignificant difference between extremely rich fens and rich *Sphagnum*-fens in pH. However, these two fen types differed significantly in water conductivity (i.e. water mineral richness). Again, slightly greater differences were revealed by log-transformed conductivity ($F = 71.128$) than by pH values ($F = 69.288$).

Context- and scale-dependence of the poor–rich gradient

At last, we shall draw attention to the next neglected issue concerning the poor–rich gradient and the fen partitioning along it: the context-dependence of any vegetation classification and ordination (e.g. Chytrý et al., 2002a, b). The character of the data-set doubtless influences the answer to the question whether the poor–rich gradient is a major ecocline in fen vegetation. In Bulgaria, the poor–rich gradient evidently controls the floristic variation of submontane fens, whereas the complete data set is governed by the altitude gradient from lowland and basin fens to subalpine fens rich in Balkan endemics. When we focus only above timberline, the major species turnover takes place along the succession gradient connected to peat accumulation (Hájková et al., 2006).

The scale-dependence is even more important in searching for vegetation-environment relationships in fens. The often reported fact that either water table (e.g. Bragazza, 1997; Dünhofen and Zechmeister, 2000) or pH and calcium (e.g. Hájek, 2002) are the major determinants of species data variation in central-European mires is strongly dependent on the scale we consider. Recent investigations in central Europe (Hájková et al., 2004) and North America (Nekola, 2004) showed that the pH/calcium gradient controls vegetation variation on the landscape scale between vegetation types, while within-vegetation-type and especially intra-site variation in pH does not significantly affect the species composition of the vegetation. On this smaller scale, water regime and organic matter content displayed a tighter relationship to the

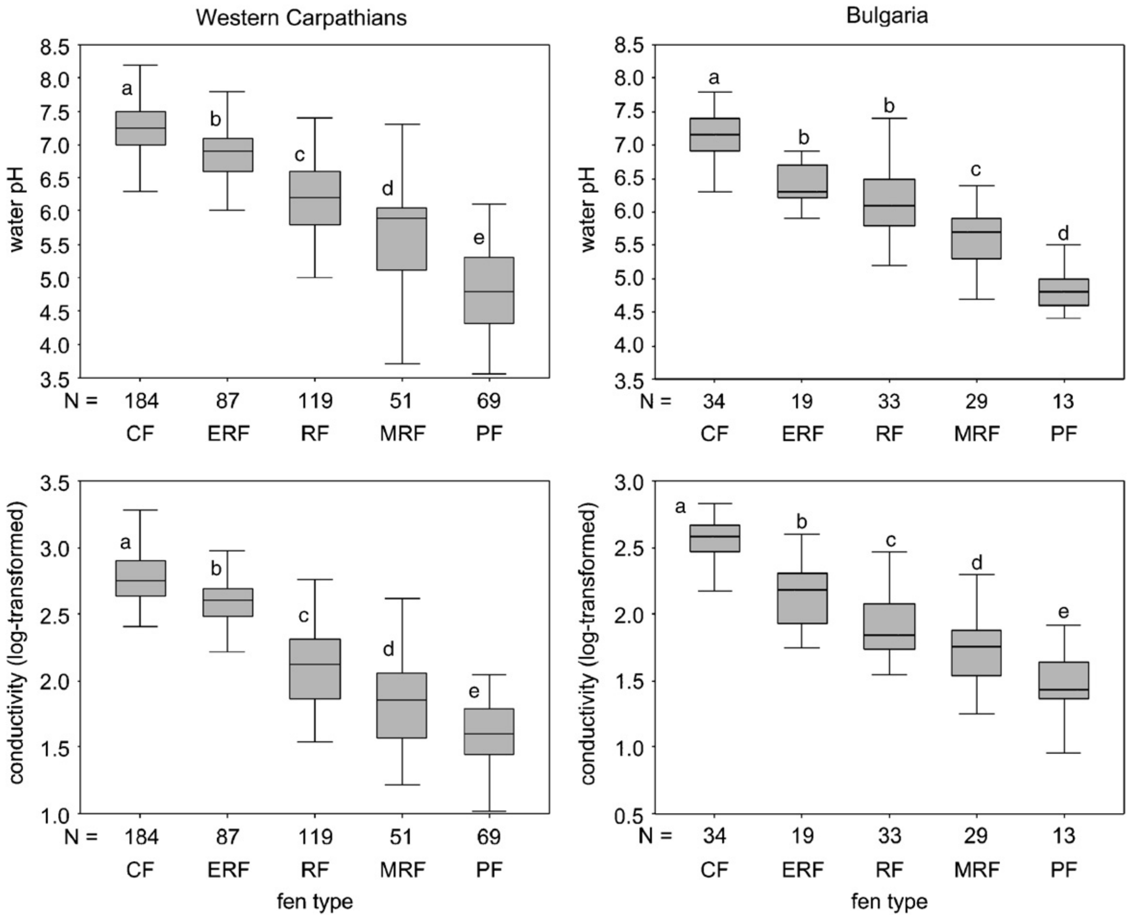

Fig. 2. Differences in water pH and conductivity between major vegetation types in submontane fens of the western Carpathians and Bulgaria. The box length is the interquartile range. The line across the box indicates the median. Significant pairwise differences (Tukey post-hoc test) are indicated by different letters. CF = calcareous tufa-forming fens; ERF = extremely-rich fens; RSF = rich *Sphagnum*-fens; MRF = modately-rich *Sphagnum*-fens; PF = poor *Sphagnum*-fens.

species-data variation. In the light of these results we should address the question whether the fen types that we propose in this paper are applicable across various scales. The standard sampling size of mires in European vegetation science is about 16 m^2 (Chytrý and Otýpková, 2003). A similar area is often used also by Fennoscandian plant ecologists (e.g. 25 m^2 by Tahvanainen, 2004). Our proposal of fen classification is therefore adjusted to the scale of square metres. However, the same fen types can be distinguished even by using extremely small plots in some cases (Hájková and Hájek, 2004a). The question remains, whether the crispness of the classification into poor–rich categories changes from small to large plots. We suppose that at the small spatial scale pH homogeneity is high, but some indicator vascular plant species are missing. Hájková and Hájek (2003) have found that correlation between vascular plant species richness and water calcium concentration is appear towards the smallest vegetation plots. The larger plots, however, can harbour a mosaic of various fen types, especially in early stages of succession from extremely rich- to rich fens. Our classification of fens does not exclude the possibility of the occurrence of various fen types in a single mire. The opposite is true: the proposed fen vegetation types are presumed to occur often, but not always, in close spatial contact.

Conclusions

An unequivocal terminology of fen vegetation types varying along the poor–rich gradient is urgently needed. Five fen-vegetation types (‘poor’, ‘moderately rich’, ‘rich’, ‘extremely rich’ and ‘calcareous’) can be distinguished rather clearly across various regions and scales. The central- and western-European syntaxonomical alliances could be integrated with the proposed fen types. The five basic fen types distinguished along the poor–rich gradient differ substantially not only in species composition of the vegetation, but also in fungal, algal and especially mollusc assemblages as well as in water chemistry. The difference between our proposal and previously used terms is that we suggest to abandon the further subdivision of poor fens and, on the other hand, to distinguish (truly) calcareous fens from extremely rich but non-calcareous ones. Calcareous fens represent an important component of the central- and southern-European landscape, especially in the Carpathians, Alps, central-European cretaceous basins and in the Balkans. They are specific and easy to delimit in terms of species composition of practically all important taxonomical groups, water chemistry, nutrient status and soil conditions. When the entire poor–rich gradient is considered, the clearest and most recognisable natural boundary between fen habitat entities is the chemical limit of the occurrence of calcitolerant *Sphagnum* species (although varying between regions and hydrological situations).

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