The structure and species richness of the diatom assemblages of the Western Carpathian spring fens along the gradient of mineral richness

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Abstract: Species composition changes along the pH and calcium gradients within wetlands were frequently studied for different groups of organisms, but few data are available for algae. Here we list 188 diatom taxa collected as epibryon and epipelon at 13 spring fens in the Western Carpathians distributed along the gradient of mineral richness. Species richness decreased along the gradient from calcareous fens to mineral–poor *Sphagnum*–fens. In agreement with fen typology based on higher plants, bryophytes, and molluscs, the same four fen types were identified. For each spring-fen type indicator diatom species were suggested. Conductivity and pH appeared to be the most important environmental factors responsible for the variation in diatom species data.

Introduction

Springs and spring fens are among the most threatened habitats across Europe. Their extinction has been accelerated by human influences such as drainage, eutrophication and changes in agricultural practices especially in the last 60 years. Despite covering a relatively small area in comparison with rivers or lakes, springs and spring fens have recently attracted the attention of biologists and conservationists due to a high share of endangered species and specialists found in their communities (e.g., Cantonati 1998, Peintinger et al. 2003, Warner & Asada 2006, Cantonati et al. 2006, Grootjans et al. 2006, Hájek et al. 2006, 2007, Payne & Mitchell 2007). Intact springs provide an opportunity to describe naturally preserved freshwater habitats (Werum 2001), however these intact springs are becoming increasingly rare. Carpathian spring fens are an excellent model habitat for studies of the variation in bryophytes, vascular plants, testaceans, and mollusc assemblages along a mineral richness gradient from extremely poor acid fens to strongly calcareous spring fens (Horsák & Hájek 2003, Hájek et

al. 2006, Opravilová & Hájek 2006). In terms of biomass production, these ecosystems are dominated by bryophytes and vascular plants (Hájková & Hájek 2003), the production of which is limited by phosphorus as compared to wet meadows which are not strongly nutrient–limited (Rozbrojová & Hájek 2008). Although microscopic diatoms are not a major contributor to biomass in spring fens, they are abundant (Poulíčková et al. 2004) and play a key role in the ecosystem functioning (Bertuzzi et al. 2006). Diatoms are used as bioindicators of water quality and past climates (Stoermer & Smol 1999).

Despite their significance, however, many aspects of the biodiversity and ecology of diatoms are poorly understood, mostly due to undersampling as compared to larger organisms (Foissner 2008). For example, in Central Europe, diatoms were studied predominantly in thermal and strongly mineral springs in the northwestern part of Bohemia (e.g. Sprenger 1930, Brabez 1941, Lederer et al. 1998, Kaštovský & Komárek 2001) and Slovakia (e.g., Bílý 1934, Hindák & Hindáková 2006, Hindák & Hindáková 2007), where specific cyanobacterial and algal assemblages were found.

Although cold, moderately mineralized springs are the most common springs in the Czech Republic and Slovakia, our knowledge on their epipelic and epiphytic algae is limited (Poulíčková et al. 2005). The aim of this study is to enhance our understanding of diatom diversity in spring fens, focussing particularly on (1) comparing the classification of diatom species data to the habitat typology based on vegetation data to see if they are in agreement (2) completing fen characterization using diatom data by providing the information on taxa diversity, occurrence of endangered and rare taxa, proportion of living and dead cells, and indicator species for each fen type, (3) determining the main environmental variables influencing the distribution of diatom assemblages, and (4) understanding differences between assemblages inhabiting different substrata (epibryon vs. epipelon).

Material and Methods

Study area and sites

The study area is located on the western margin of the Western Carpathians. It stretches along the border between the Czech Republic and Slovakia, including the White Carpathian Mts. in the south and the Beskydy Mts. and the Turzovská vrchovina Mts. in the north. This region forms a part of the flysch belt, in which sandstone and clay of variable calcium content alternate. The chemical composition of groundwater reflects the bedrock chemistry, varying from carbonatogenic waters rich in calcium, sodium and potassium and supporting travertine (tufa) formation in the south of the study area, to acidic waters rich in iron, silica, and sulphates and poor in all other elements in the northernmost part of the study area. The geological structure and chemical characteristics of the area studied were described in detail by Hájek et al. (2002). Water chemistry substantially influences the spring fen biota, thus mineral richness is the most important ecological gradient in these habitats (the poor-rich gradient sensu Malmer 1986). Along this gradient, four habitat types based on vegetation were identified: (1) calcareous fens with tufa formation (petrifying springs), (2) extremely mineral-rich fens without tufa formation, (3) moderately rich and rich *Sphagnum*–fens, and (4) mineral–poor acid *Sphagnum*–fens (Hájek et al 2006). On the basis of previous studies set in Western Carpathian spring fens we chose 13 sites differing in water chemistry. Nine sites were selected within spring fens with a different degree of calcium carbonate precipitation and four within *Sphagnum*–fens in order to obtain a representative set of habitat types (Fig. 1).

Sampling and laboratory methods

Algal samples were collected at two main microhabitat types: epibryon (26 samples) and epipelon (13 samples) in May 2006. Epilithon was found in only 5 out of the 13 sites, therefore it was not included in this study. Altogether three samples were collected at each site: 1 sample of epipelon (1.5 ml) taken with a pipette and 2 samples of different bryophyte tufts taken by cutting with scissors. In the laboratory, each bryophyte sample was weighed, then washed in 20 ml of distilled water and thoroughly squeezed. Each algal sample was fixed with 4% formaldehyde and stored in a container. After drying, bryophytes were weighed again. The water content was estimated as the mass difference between the dry and the fresh bryophyte matter following the method used by Poulíčková et al. (2005). To assess relative representation of all algal groups (including Cyanoprokaryota), 400 individuals from each sample were counted in the CYRUS I counting chamber. In the course of counting, living (containing protoplast) and dead (empty frustule) diatom cells were distinguished. Subsequently, permanent slides of diatoms were prepared following the hydrogen peroxide method (Ettl 1978). Samples were treated with 30% H_2O_2 and HCl in order to clean diatom frustules and to remove $CaCO_3$. Diatom frustules were mounted in Pleurax. In each permanent slide 400 diatom valves were counted using the Nikon E 400 Eclipse microscope. Diatoms were identified mainly according to Krammer & Lange–Bertalot (1986, 1988, 1991 a,b), along with Krammer (2000, 2002), Lange–Bertalot (2000) and Werum & Lange–Bertalot (2004). Photomicrography was carried out using the Zeiss Axioimager with the Zeiss Axiocam HRc digital camera (Carl Zeiss, Jena). Images were captured and managed using the Zeiss Axiovision Version 4.5 imaging software. Differential interference contrast (DIC) optics was used at ×100 (planapochromat lens, nominal numerical aperture 1.4 and 0.95).

Water conductivity and pH were measured in situ by portable instruments (WTW Multi 340i/SET). For characterizing each site one–shot samples of water were taken in October 2006. Water samples were collected in autumn due to relative stability of water chemistry (Hájek et al. 2002). The concentrations of major ions (Table 5) were measured in an accredited laboratory (for details see Hájek & Hekera 2004).

Statistical analyses

The species abundance (n) was log–transformed as $Y = \log (n+1)$ and classified by the cluster analysis using Group average (UPGMA) and Euclidean distance. Indicator species analysis based on this classification was computed. For cluster analyses and indicator species analyses the PC–ORD package (McCune & Mefford 1999) was used. Detrended Correspondence Analysis (DCA) was used to study relationships between species composition and measured variables. Spearman rank correlation (r_s) and Mann–Whitney U test were used

Table 1. Number of taxa recorded in individual fen types and Median number of proportions (%) of dead cells.

	Group 1	Group 2	Group 3	Group 4
Total number of taxa recorded	114	107	48	62
Median number of taxa per sample	35	34	28	18
Median number of proportions of dead cells per sample	27	30	17	16

Fig. 1. Map of studied sites.

Results

to examine possible relationships between explanatory variables and site scores on the first three ordination axes. Bonferroni corrections of the significance level were used for multiple comparisons of environmental variables (HOLM 1979). The CANOCO 4.5 package (TER BRAAK & ŠMILAUER 2002) was used for DCA techniques and STATISTICA 8 (HILL & LEWICKI 2007) for the other (uni–dimensional) analyses.

Results

Altogether 188 diatom taxa mostly belonging to pennate diatoms were found (Table S1, Figs 6, 7). The only centric species, *Aulacoseira distans,* appeared at one site only. One third of the taxa identified (61 taxa) are cited in the Red List of freshwater diatoms of Germany (LANGE–BERTA-LOT 1996) under various categories: endangered (5 taxa), vulnerable (10 taxa), susceptible (8 taxa),

and near threatened (24 taxa). Rare species mostly occurred in very small abundance in samples; nevertheless *Eunotia steineckei* was very abundant in three samples. Most of the rare species were present in only one fen type (see below), but some of them, such as *Diploneis petersenii, Encyonema lunatum* agg., *Eunotia* cf *inflata, E. tetraodon, E. steineckei, Navicula tridentula, Placoneis ignorata, Rossithidium petersenii,* and *Stauroneis acuta,* occurred in two or more fen types.

On the basis of cluster analysis based on relative frequencies of diatoms in samples, the samples were classified into four groups (Fig. 2). The first cluster consisted solely of samples from extremely mineral–rich fens with tufa formation (calcareous fens). In total, 114 taxa were found at these sites, the median number of taxa per sample was 35 (Table 1). *Achnanthidium minutissimum* agg. was the most abundant diatom in this cluster.
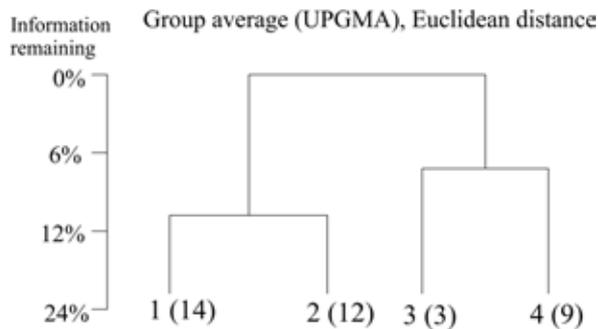
Fig. 2. Cluster analysis of diatom assemblages based on relative frequence data (log-transformation, Euclidean distance, Group average (UPGMA). Numbers of samples in each cluster are given in parentheses. Spring fen types: (1) calcareous fens; (2) brown-moss fens; (3) mineral-rich *Sphagnum*-fens; (4) mineral-poor *Sphagnum*-fens.

Eucocconeis laevis, the species with the highest indicator value within the tufa fens (Table 2), occurred only in this fen type. One of the typical genera of these high productive calcareous fens, *Cymbella* s.l., achieved the highest abundance and diversity along the whole poor–rich gradient. The following rare species were present: *Campylodiscus hibernicus*, *Cocconeis* cf *neodiminuta*, *Navicula pseudobryophila*, *N. pseudokotschyi*, *Stauroneis tackei*, *Surirella helvetica*, and *S. spiralis*. The second cluster included mineral–rich brown-moss fens. Diatom assemblages were also very diverse, with composition similar to the previous fen type. Altogether 107 taxa were found and the median number of taxa per sample was 34. The most abundant taxon *Planothidium lanceolatum* agg. was the indicator with the highest indicator value. In this cluster, the araphid diatoms *Fragilaria* sp. div. were the most abundant and diverse within the gradient of mineral richness. Rare and interesting taxa were represented by *Cavinula cocconeiformis*, *Decussata placenta*, *Gomphonema lagerheimii*, *Pinnularia brandeliformis*, *Psammothidium ventrale*, and *Stauroneis gracillima*. The third cluster represented a rare spring fen type, mineral–rich *Sphagnum*-fens. The total number of taxa recorded (48 taxa) was lower than in the following type of *Sphagnum*–fens, however the median number of taxa per sample was higher (28 taxa). The total number of taxa may be underestimated because the number of samples in this cluster was very low. *Chamaepinnularia mediocris* had the highest indicator value. The rare species *Naviculadicta digitulus* occurred in this fen type. The fourth cluster consisted of mineral–poor acid *Sphagnum*–fens which were inhabited by

species poor diatom assemblages. Sixty–two taxa were recorded and the median number of taxa per sample was 18. The most abundant species *Eunotia exigua* var. *tenella* was found in all samples, as was *Eunotia incisa*. Both species were good indicators for the biotope of *Sphagnum*–fens. The following rare species were present: *Eunotia monodon*, *E. nymanniana*, *Neidium bisulcatum*, *N. hercynicum*, and *Stenopterobia delicatissima*.

Diatoms dominated in all algal samples collected in all types of fens. The highest proportion of diatoms was found in calcareous fens (Fig. 3). The percentage of living diatom cells was at least 50% in all samples. The lowest proportions of dead diatom cells were recorded in samples from mineral–poor *Sphagnum*–fens (Table 1).

The DCA revealed a continuous change of the diatom assemblages along the first ordination axis from extremely mineral–rich fens to poor acid fens (Fig. 4). Of the three ordination axes, the first explained 14% of the variation in the species data, while the second explained 5%, and the third explained only 3.3%. These results were in accordance with the result of the cluster analysis (Fig. 2) and with the correlations of explanatory variables with the sample scores. The variables describing the poor–rich gradient (i.e. pH, Ca^{2+}, Fe, Si, NO_3^-, and conductivity) were significantly correlated (P<0.004) with the position of samples along the first ordination axis (Tables 3, 4). The position of individual diatom species in the DCA diagram reflected the relation of species to pH. On the left side there were alkalibiont and alkaliphilous species and on the right side there were acidobiont and acidophilous species. In the middle of the scatter there were common
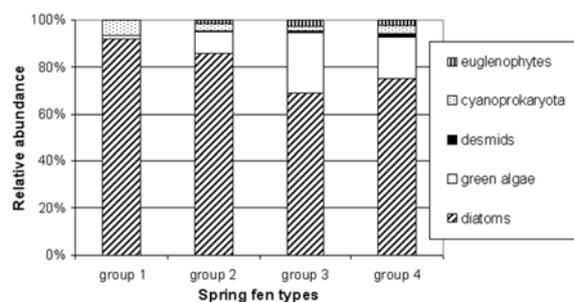

Fig. 3. Relative abundance of individuals of algal groups found in four groups of fens: (1) extremely mineral–rich fens with tufa precipitation (calcareous fens); (1) calcareous fens; (2) brown–moss fens; (3) mineral–rich *Sphagnum*–fens; (4) mineral–poor *Sphagnum*–fens.

(*Achnanthidium minutissimum* agg., *Gomphonema clavatum* agg., *G. parvulum*, *Meridion circulare*, *Navicula cryptocephala*, *N. cryptotenella*, *Planothidium lanceolatum* agg., and *Sellaphora pupula*) and euryvalent (*Adlafia minuscula*, *Gomphonema angustatum* agg., and *Eunotia minor*) species (Fig. 5). The number of species decreased significantly from mineral–rich to mineral-poor sites. The first ordination axis was also correlated with mean depth of water measured in the centre of each spring fen site. The second ordination axis separated bryophyte samples from tufa–forming fens (the lower part of the diagram) and other samples, including epipelon samples from tufa-forming fens and both epipelon and bryophyte samples from all remaining spring fen types. This dissimilarity of epibryon of calcareous fens resulted in significant difference (Mann–Whitney U test; P<0.05) between epipelon and epibryon on the second ordination axis. The sample scores on the third ordination axis were correlated with the mean discharge. Water content in samples, shading of spring fens, and water temperature did not display any significant correlation.

Discussion

The typology of the central European spring fens based on the species composition of the vegetation reflects water chemistry of spring water (Hájek et al. 2006). This classification can be used across various regions and scales. Analogous changes in species composition along the poor-rich gradient have also been observed in molluscan (Horsák & Hájek 2003), fungal (Vašutová 2005), testacean (Opravilová & Hájek 2006), and algal (Poulíčková et al. 2003) assemblages. In the previous research focused on spring fen algae (Poulíčková et al. 2003), however, samples of epiphytic diatoms were classified only according to phytosociological classification and no numerical classification was done on the diatom species data (Poulíčková et al. 2003). Our results based directly on diatom data showed the same pattern as the results of the phytosociological approach. The variability of diatom assemblages was governed by a strong environmental gradient of pH, calcium, and conductivity. These geochemical factors were also found to be the most important environmental variables influencing the structure and composition of diatom assemblages in various types of springs and small wetlands occurring

along spring brooks (e.g. Cantonati 1998, Cantonati et al. 2006, Kapetanovic & Hafner 2007).

The samples used for this study were collected during spring which is considered to be the season of the highest diatom diversity (e.g., Cantonati 1998, Hafner 2008). The species richness of diatoms was high in extreme mineral–rich tufa–forming spring fens and decreased towards acid mineral–poor fens. The same pattern has already been observed in studies focused on vascular plants, bryophytes, and molluscs of spring fens (Hájek et al. 2002, Hájková & Hájek 2003, Horsák & Hájek 2003, Tahvanainen 2004). On the other hand, no correlation of species richness with the poor–rich gradient has been documented on aquatic invertebrates (stoneflies and testaceans) and fungi (Vašutová 2005, Opravilová & Hájek 2006, Bojková & Helešic in press). Tufa–forming spring fens recorded the highest number of taxa and hosted very diverse diatom assemblages which consisted not only of alcaliphilous and alcalibiont taxa (e.g., *Amphora normannii*, *Gomphonema angustum*, and *Caloneis constans*, typical inhabitants of sites with strong tufa precipitation), but also several halophilous (e.g., *Navicula phyllepta* and *Nitzschia dubia*) and xerotolerant species. The presence of halophilous species in this habitat was observed in mollusc and vascular plants communities as well (Cooper 1995, Horsák 2006, Dítě et al. 2007). The calcareous spring fens and salt-rich wetlands share several attributes, such as high alkalinity, high mineral richness, and high concentration of sulphate salts. The latter is typical of the Bílé Karpaty Mts., where high concentration of sulphates is caused by the oxidation of pyrite contained in the bedrock claystones (Hájek & Hekera 2005). As the content of silica in spring fen water increased along the poor–rich gradient, diatom frustules in samples from petrifying spring fens were often poorly silicified, which made identification difficult at times. Although silica is crucial for building diatom frustules, its concentrations in calcareous fens were not as low to limit diatom development. High species richness of vegetation in mineral–rich sites has been explained by a large calcicole species pool resulting from historical and evolutionary processes (Pärtel 2002, Chytrý et al. 2003). Historical processes connected with species pool evolution in relation to historical habitat commonness (Hájek et al. 2007) thus override the physiological effects inherent to particular groups of organisms. This finding may also help to understand patterns in other organ-

Table 2. Results of indicator species analysis [(1) calcareous fens; (2) brown–moss fens; (3) mineral–rich *Sphagnum*–fens; (4) mineral–poor *Sphagnum*–fens]. Indicator value (Ind. val.) and p–value (** P<0.01; * P<0.05) are shown. Only taxa with Indicator value higher than 40 are shown.

Group 1 Calcareous fens		Group 2 Brown-moss fens		Group 3 Mineral-rich *Sphagnum*-fens		Group 4 Acid *Sphagnum*-fens	
Taxon	Ind. val.	Taxon	Ind. val.	Taxon	Ind. val.	Taxon	Ind. val.
Achnanthes laevis	79**	*Planothidium lanceolatum* agg.	66**	*Chamaepinnularia mediocris*	72**	*Eunotia incisa*	92**
Gomphonema angustum	79**	*Gomphonema clavatum*	62**	*Eunotia steineckii*	66**	*Frustulia crassinervia*	89**
Surirella brebissonii	69**	*Navicula cryptocephala*	58**	*Adlafia aquaeductae*	55**	*Eunotia paludosa*	83**
Cymbella austriaca	64**	*Psammothidium subatomoides*	50**			*Eunotia exigua var. tenella*	77**
Delicata delicatula	57**	*Diploneis ovalis*	47**			*Neidium hercynicum*	67**
Nitzschia linearis	55**	*Encyonopsis microcephala*	59*			*Tabellaria flocculosa* s.l.	67**
Nitzschia amphibia	50**	*Placoneis ignorata*	44*			*Brachysira brebissonii*	65**
Gomphonema angustatum agg.	43**					*Pinnularia subcapitata*	51*
Achnanthidium minutissimum	40**						
Cymbella affinis	46*						
Encyonopsis cesatii	55*						
Cymbella subaequalis	49*						
Denticula tenuis	47*						
Cocconeis placentula	47*						
Caloneis alpestris	43*						
Encyonopsis microcephala	43*						
Amphora pediculus	42*						
Navicula cryptotenella	41*						
Stauroneis smithii	41*						

isms where physiological and historical effects are shared. Molluscan assemblages, for example, display steep increase in species richness towards calcium–rich habitats (Horsák & Cernohorsky 2008), which is most often explained by physiological demands.

On the opposite end of the gradient, mineral–poor *Sphagnum*–fens were inhabited by species-poor assemblages characterized by a high share of green algae in samples. Low species richness was also reported by authors who studied diatoms of peat bogs (e.g., Lederer et al. 1998, Lederer 1999) or epiphytic diatoms on different *Sphagnum*–species (e.g., Nováková & Poulíčková 2004, Buczkó 2006). In the most extreme acidic sites diatoms were not even present at all (Buczkó 2006). *Brachysira brebissonii, Eunotia incisa, E. paludosa, E. steineckei, E. ex-*
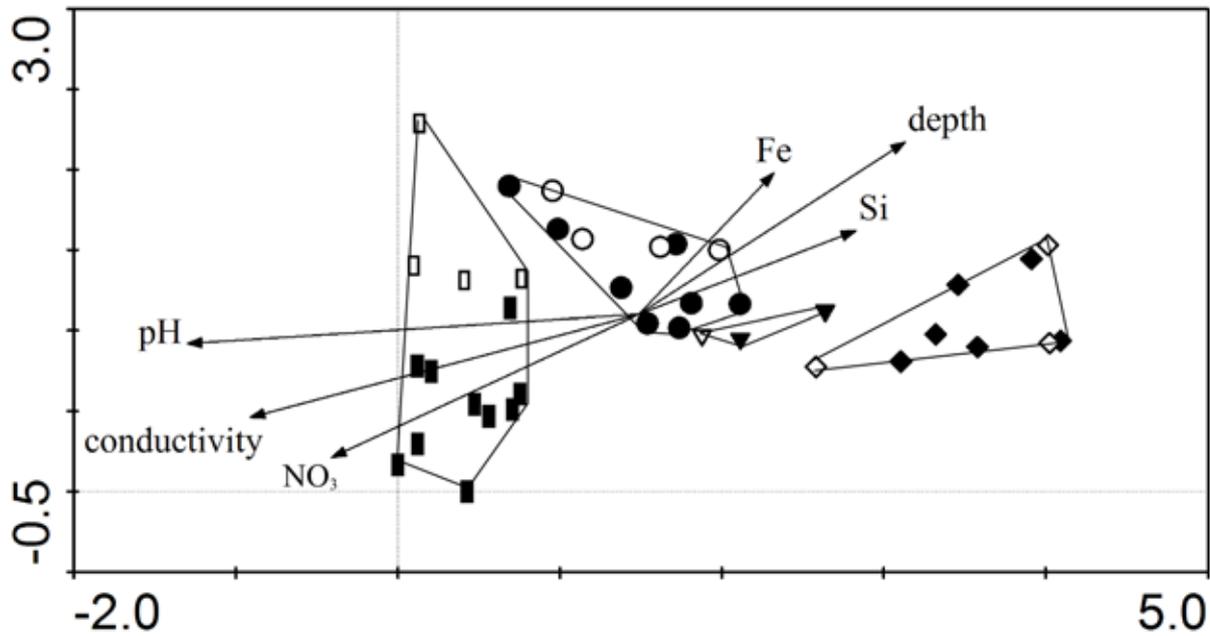
Fig. 4. DCA diagram of samples on the first two ordination axes with posteriori plotted explanatory variables; only those significantly correlated with the first two ordination axes were used (see Table 2). Following symbols were used: calcareous fens (rectangle), brown–moss fens (circle), mineral–rich *Sphagnum*–fens (triangle), mineral–poor *Sphagnum*–fens (diamond); black symbols (epibryon); white symbols (epipelon).
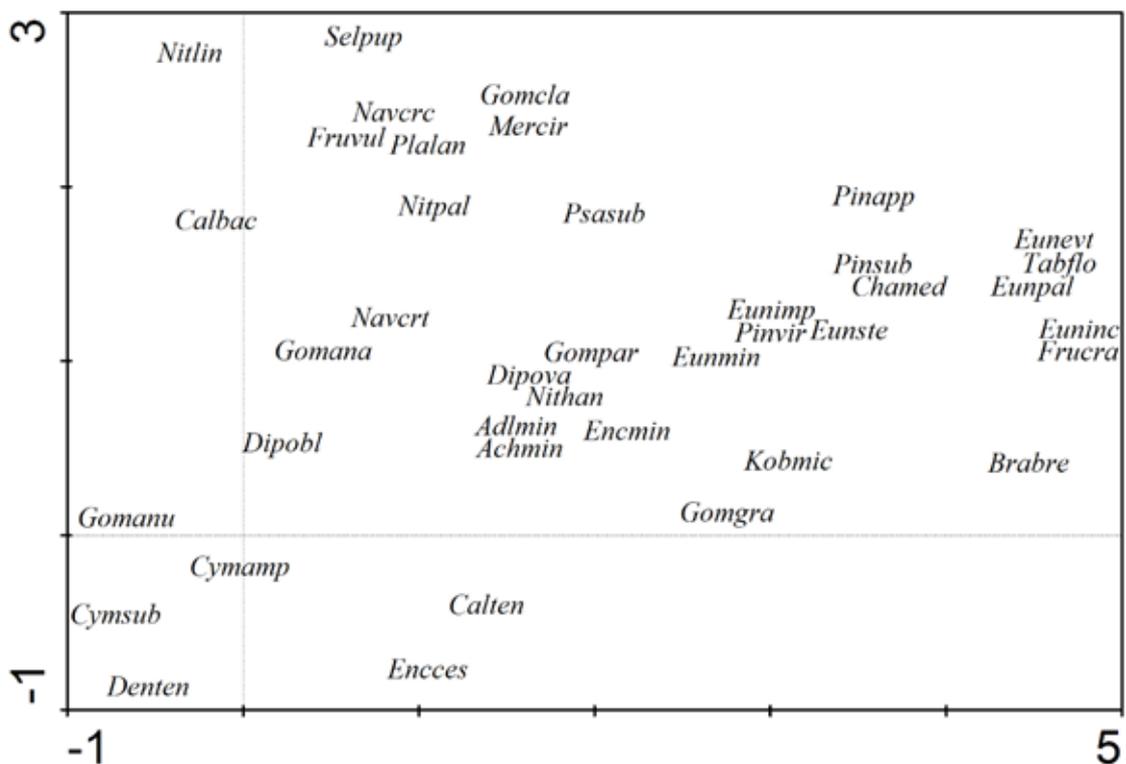

Fig. 5. DCA diagram of species on the first two ordination axes. Abbreviations: Achmin *Achnanthidium minutissimum* agg., Adlmin *Adlafia minuscula*, Brabre *Brachysira brebissonii*, Calbac *Caloneis bacillum*, Calten *C. tenuis*, Dipova *Diploneis ovalis* agg., Encces *Encyonopsis cesatii*, Eunevt *Eunotia exigua* var. *tenella*, Eunimp *E. implicata*, Euninc *E. incisa*, Eunpal *E. paludosa*, Eunste *E. steineckii*, Gomana *Gomphonema angustatum* agg., Gomanu *G. angustum*, Gomcla *G. clavatum* agg, Gomgra *G. gracile*, Gompar *G. parvulum*, Kobmic *Kobayasiella* cf *micropunctata*, Mercir *Meridon circulare*, Navcrc *Navicula cryptocephala*, Navcrt *N. cryptotenella*, Nithan *Nitzschia hantzschiana*, Nitlin *N. linearis*, Nitpal *N. palea*, Pinvir *Pinnularia viridis* agg., Plalan *Planothidium lanceolatum* agg., Psasub *Psammothidium subatomoides*, Tabflo *Tabellaria flocculosa* agg.

Table 3. Relationships between all variables and sample scores on the first three ordination axes. Significant values of Spearman rank correlations (r_s) and their probabilities (P) are given. After using Bonferroni corrections the current cut level was P = 0.004.

DCA axis	1		2		3	
	r_s	P	r_s	P	r_s	P
pH	-0.95	<0.004	-0.24	-	0.07	-
Conductivity	-0.86	<0.004	-0.33	-	-0.09	-
Average discharge	-0.39	-	-0.11	-	0.52	<0.004
Water depth	0.70	<0.004	0.52	<0.004	-0.07	-
Si	0.54	<0.004	0.14	-	-0.01	-
Water content	0.27	-	0.43	-	-0.6	-
Shading	0.41	-	0.37	-	-0.08	-
Ca^{2+}	-0.89	<0.004	-0.13	-	0.06	-
Fe	0.47	<0.004	0.53	<0.004	0.08	-
NO_3^-	-0.72	<0.004	-0.20	-	0.13	-
Temperature	0.13	-	0.29	-	0.13	-
Number of taxa	-0.51	<0.004	-0.03	-	-0.02	-

igua var. *tenella*, *Chamaepinnularia mediocris*, *Kobayasiella* spp., *Pinnularia subcapitata*, and *Tabellaria flocculosa* often recorded in mire habitats (e.g., VAN DE VIJVER & BEYENS 1997, BUCZKÓ 2003, 2006, POULÍČKOVÁ et al. 2004, KAPETANOVIC & HAFNER 2007) were frequent and abundant in *Sphagnum*-fens. Comparing with other groups of spring fens, the assemblages of *Sphagnum*–fens comprised a lower share of dead diatoms. It might be caused by the dissolution of empty frustules at very low pH, which was already observed for testate amoebae shells (MITCHELL et al. 2008).

Along the gradient of mineral richness several taxa exhibiting high morphological variation were recorded. Furthermore, identification was difficult for transitional types between particular species (e.g., *E. exigua*/*E. exigua* var. *tenella*, *Eunotia implicata*/*E. minor*, and *Gomphonema tergestinum*/*Reimeria sinuata*). In such problematic cases geometric morphometrics should be used as a helpful tool in distinguishing diatom morphospecies (e.g., FRÁNKOVÁ et al. 2009). There were also aggregates (heterogenous complexes) containing several to many entities that may be regarded as semicryptic or cryptic species (see also MANN et al. 2004, LUNDHOLM et al. 2006). For example, *Achnanthidium minutissimum* agg. occurred along the whole gradient.

The differences in the structure of diatom assemblages between two main microhabitats, i.e. sediment and bryophytes, were observed only in tufa–forming spring fens. Sediment was preferred mostly by diatoms with larger frustules (e.g., *Nitzschia dubia*, *N. linearis*, and *Ulnaria ulna*), whereas bryophyte tufts, especially those with small water content, often hosted xerotolerant species (e.g., *Caloneis tenuis* and *Encyonopsis cesatii*). Distinct dissimilarity of epibryon of calcareous fens was probably related to the structural features of these sites, which were shallow and bryophytes were not as waterlogged as in peat–forming fens. Although we sampled three microhabitats differing in moisture (measured as water content), it did not have a significant influence. This was probably due to the fact that water chemistry was responsible for majority of the variation in species richness and composition on a larger scale, and thus heterogeneity of moisture then seems to be more important at the within–site scale.

The Western Carpathian spring fens are unique biotopes harbouring a diverse and species–rich diatom flora with extraordinary high portion of oligotraphentic species and "Red List taxa". The proportion of Red List taxa (32% of 188 taxa recorded) was identical to German and Swiss springs (WERUM & LANGE–BERTALOT 2004, TAXBÖCK & PREISIG 2007); higher proportion of threatened taxa (up to 70%) was found in springs

Table 4. Physical–chemical characteristics of particular groups of sites.

|	Group 1 Calcareous fens			Group 2 Brown–moss fens			Group 3 Mineral–rich *Sphagnum*–fens			Group 4 Acid *Sphagnum*–fens		
	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max
pH	8.0	6.5	8.8	7.0	5.8	8.5	6.3	5.3	6.9	5.3	2.8	8.1
temperature (°C)	10.9	5.0	17.0	11.1	7.0	19.0	12.1	9.0	16.0	12.6	6.0	25.0
conductivity ($\mu S\ cm^{-1}$)	439	252	634	142	48	354	84	67	150	55	30	114
dissolved oxygen ($mg\ l^{-1}$)	7.7	1.7	12.7	6.1	0.3	9.8	5.9	3.5	8.1	4.8	0.1	9.7
discharge ($ml\ s^{-1}$)	265	33	1000	72	17	200	89	50	167	146	17	500
PO_4^{3-} ($mg\ l^{-1}$)	0.1	0.1	0.5	0.2	0.1	0.7	0.2	0.1	0.4	0.2	0.1	0.4
SO_4^{2-} ($mg\ l^{-1}$)	34.8	16.4	50.2	13.8	3.5	21.4	11.3	5.9	13.8	7.3	5.7	11.0
NO_3^- ($mg\ l^{-1}$)	6.5	0.1	12.7	1.2	0.1	3.2	2.3	0.2	5.5	0.3	0.1	0.6
Si ($mg\ l^{-1}$)	6.9	5.5	8.3	10.7	6.9	13.8	11.0	9.8	15.6	12.3	9.6	15.6
Fe ($\mu g\ l^{-1}$)	207	29	816	1482	69	6340	2570	540	4750	947	46	2090
Mn ($\mu g\ l^{-1}$)	31	2	167	82	4	278	75	24	163	55	20	158
Ca ($mg\ l^{-1}$)	83.6	60.6	112.0	24.0	8.6	50.0	6.4	2.9	9.0	4.0	2.1	5.4
Mg ($mg\ l^{-1}$)	10.0	2.4	17.0	6.8	1.2	15.5	1.8	1.0	2.5	1.6	0.7	3.1
Na ($mg\ l^{-1}$)	10.3	3.8	22.6	7.8	2.0	17.7	5.2	1.1	11.5	6.8	2.8	11.0
K ($mg\ l^{-1}$)	4.1	1.0	8.7	3.3	0.5	8.3	3.4	1.0	9.7	2.7	1.1	4.4
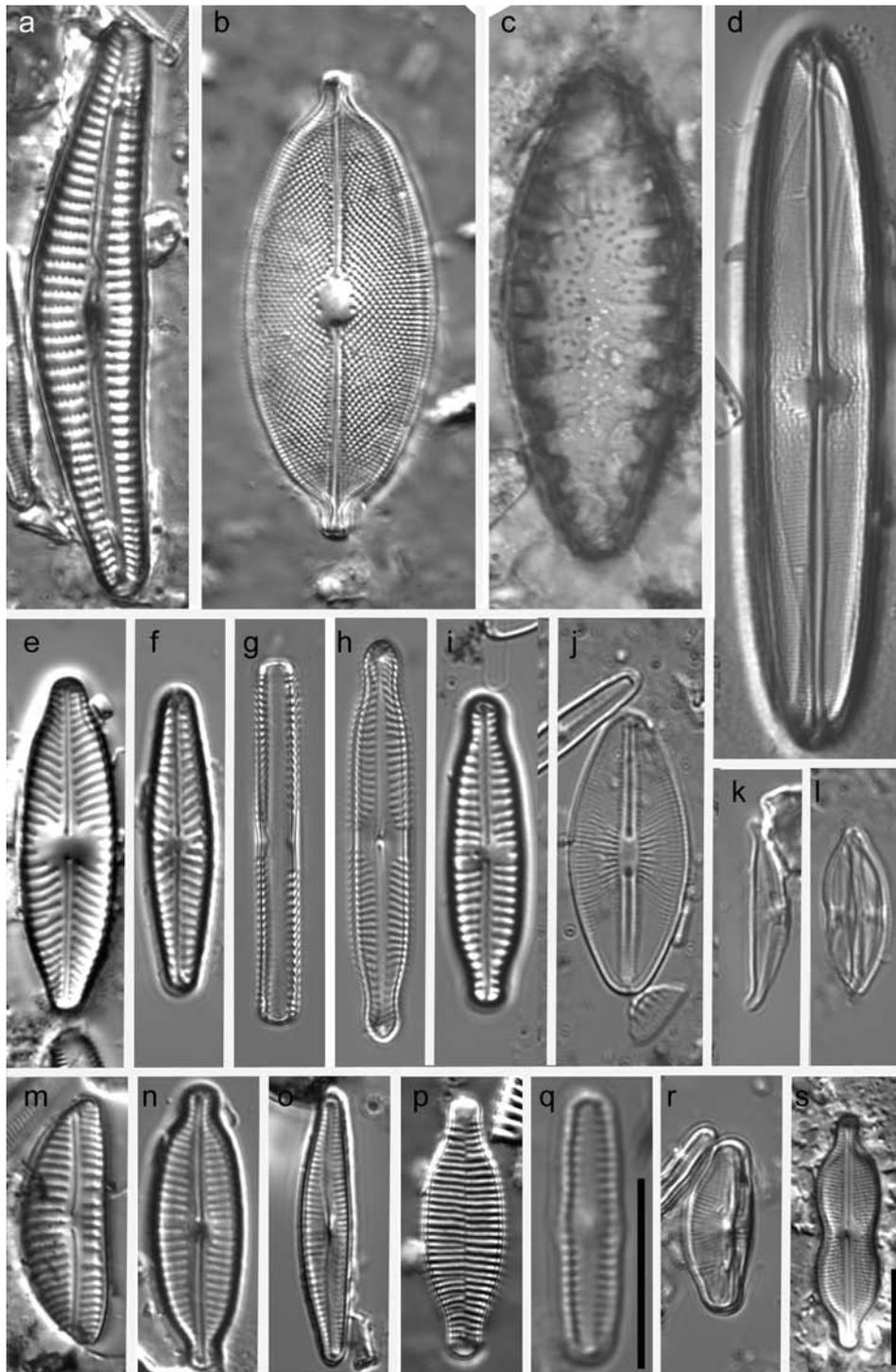
Fig. 6. (a) *Cymbella affinis*, (b) *Decussata placenta*, (c) *Surirella helvetica*, (d) *Neidium hercynicum*, (e) *Placoneis ignorata*, (f) *Navicula seibigiana*, (g, h) *Pinnularia subcapitata*, (i) *Gomphonema productum*, (j) *Cavinula cocconeiformis*, (k, l) *Amphora montana*, (m) *Encyonema minutum*, (n) *Cymbella amphicephala*, (o) *Delicata delicatula*, (p) *Fragilaria virescens*, (q) *Chamaepinnularia mediocris*, (r) *Eucocconeis laevis*, (s) *Neidium binodeforme.* Scale bars 10 μm (s – scale bar for all images except of image q)

and mires of the Alps (CANTONATI 1998, 2006, CANTONATI & SPITALE 2009). The value of these habitats is also underlined by the absence of invasive species, such as *Didymosphenia geminata* (LYNGBYE) M. SCHMIDT which is widespread in the running waters of the Beskydy Mts (GÁGYOROVÁ & MARVAN 2002).
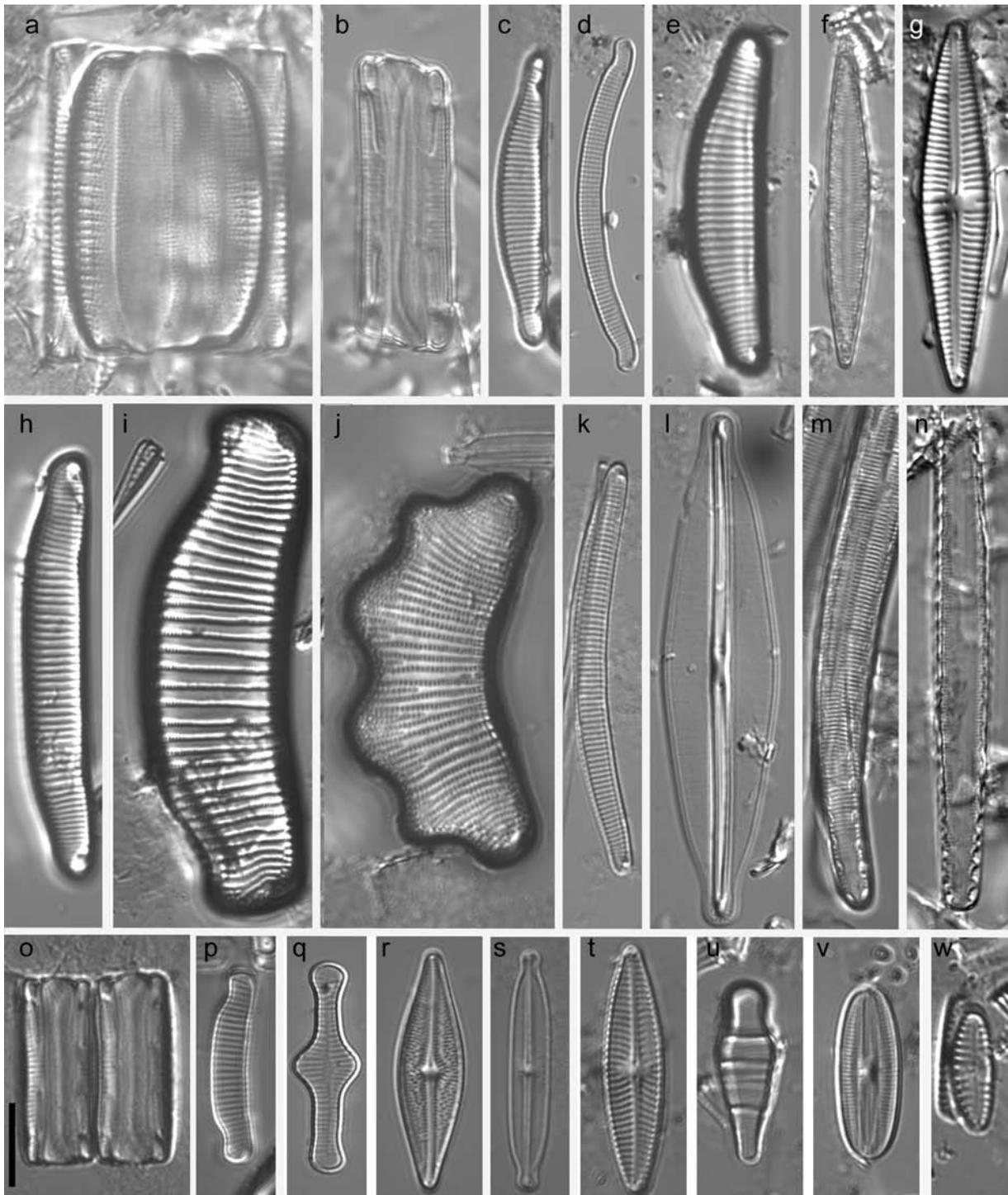
Fig. 7. (a) *Eunotia soleirolii*, (b, c) *E. incisa*, (d) *E. steineckei*, (e) *E. minor*, (f, n) *Stenopterobia delicatissima*, (g) *Gomphonema* cf *hebridense*, (h) *Eunotia soleirolii*, (i) *E.* cf *inflata*, (j) *E. tetraodon*, (k) *E. bilunaris*, (l) *Frustulia crassinervia*, (m) *Stenopterobia* cf *curvula*, (o, p) *Eunotia exigua* var. *tenella*, (q) *Tabellaria* cf. *ventricosa*, (r) *Brachysira* sp., (s) *Kobayasiella* cf *micropunctata*, (t) *Navicula cryptotenella*, (u) *Meridion constrictum*, (v) *Diploneis petersenii*, (w) *Reimeria sinuata*. Scale bar 10 μm.

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Supplementary material

the following supplementary material is available for this article:

Table S1. List of all recorded diatom taxa and their distribution within four main groups of fens.

This material is available as part of the online article (http://fottea.czechphycology.cz/contents)

Table S1. List of all recorded diatom taxa and their distribution within four main groups of fens: (1) calcareous fens (14 samples); (2) brown-moss fens (12 samples); (3) mineral-rich *Sphagnum*-fens (3 samples); (4) mineral-poor *Sphagnum*-fens (9 samples). The total number of individuals of particular species in samples/the number of its occurrence within each group are given.

Taxon	Comments	Groups of fens			
		1	2	3	4
Achnanthidium minutissimum agg.		2875/14	774/12	252/3	151/6
Achnanthes sp. 1		5/4	102/10	12/1	2/1
Achnanthes sp. 2		6/2	13/2		1/1
Achnanthes sp. 3		1/1			
Achnanthes sp. 4		1/1			
Achnanthes sp. 5				1/1	
Achnanthes sp. 6				7/1	
Achnanthes sp. 7		1/1			
Achnanthes sp. 8			4/1		
Achnanthes sp. 9			24/1		
Adlafia aquaeductae (Krasske) Moser, Lange-Bert. et Metzeltin				6/1	
Adlafia minuscula (Grunow) Lange-Bertalot		39/13	38/4	18/3	5/2
Amphipleura pellucida Kützing		7/2			
Amphora copulata (Kützing) Schoeman et Archibald		9/3	6/3		
Amphora montana Krasske		24/3			
Amphora normannii Rabenhorst		2/2			
Amphora ovalis (Kützing) Kützing		1/1			
Amphora pediculus (Kützing) Grunow		30/1	1/1		1/1
Amphora sp. 1		2/1			
Aulacoseira distans (Ehr.) Simonsen					95/3
Brachysira sp.				1/1	168/6
Brachysira sp.			2/1		
Brachysira vitrea (Grunow) Ross in Hartley				1/1	27/3
Caloneis alpestris (Grunow) Cleve		11/6			
Caloneis bacillum (Grunow) Cleve	Some individuals resembled *Caloneis constans* Reichardt.	32/10	23/6	1/1	
Caloneis tenuis (Gregory) Krammer		223/7	2/2	4/2	5/2
Campylodiscus hibernicus Ehrenberg		4/2			
Cavinula cocconeiformis (Gregory ex Greville) Mann et Stickle			7/3		
Chamaepinnularia mediocris (Krasske) Lange-Bertalot			122/2	209/3	39/8
Cocconeis cf *neodiminuta* Krammer		2/2			
Cocconeis placentula C.G. Ehrenberg	including varieties *euglypta, lineata,* and *placentula*	15/9	3/2		1/1
Cymbella affinis Kützing		18/8			3/1
Cymbella amphicephala Naegeli		30/7	5/2	3/1	1/1
Cymbella austriaca Grunow in A. Schmidt et al.	including *Cymbopleura austriaca* (Grunow) nov. comb. and *Cymbopleura subaustriaca* (Grunow) Krammer	28/9			

Species	Notes				
Cymbella laevis Naegeli		4/1			
Cymbella lanceolata (Agardh) Agardh		1/1	1/1		
Cymbella subaequalis Grunow		30/9	6/3		
Decussata placenta (Ehrenberg) H. Lange-Bertalot			9/3		
Delicata delicatula (Kützing) Krammer		67/8			
Denticula tenuis Kützing		93/7			1/1
Diadesmis sp. 1		12/4	2/2		
Diatoma anceps (Ehrenberg) Kirchner			5/2	1/1	
Diploneis elliptica (Kützing) Cleve		3/2	3/1		
Diatoma hyemalis agg.	including *Diatoma hyemalis* (Roth) Heiberg and *D. mesodon* (Ehrenberg) Kützing	1/1	4/2		
Diploneis oblongella (Naegeli) Cleve-Euler		36/11	26/5	3/1	
Diploneis ovalis agg.	including *Diploneis fontanella* Lange-Bertalot, *D. fontium* Reichardt et Lange-Bertalot and *D. krammeri* Lange-Bertalot et Reichardt	19/8	44/10	3/1	4/3
Diploneis petersenii Hustedt		10/4	5/3	1/1	3/2
Encyonema lunatum agg.	including *Encyonema neogracile* Krammer and *E. lunatum* (W. Smith) Van Heurck		8/4	3/2	18/5
Encyonema minutum agg.	including *E. minutum* (Hilse in Rabenhorst) D.G. Mann, *E.silesiacum* (Bleisch ex Rabenh.) D. G. Mann in Round, Crawford & Mann, and *E.ventricosum* Kützing	2/2	94/7	7/1	1/1
Encyonopsis cesatii (Rabenhorst) Krammer		177/11		6/1	23/2
Encyonopsis microcephala (Grunow) Krammer		16/6			
Eucocconeis laevis (Kützing) Meister		29/11			
Eunotia bilunaris (Ehrenberg) Mills var. *bilunaris*		2/1	11/4		1/5
Eunotia exigua (Brebisson ex Kützing) Rabenhorst var. *exigua*			10/4		
Eunotia exigua var. *tenella* (Grunow) Nörpel et Alles			3/3	12/3	1266/9
Eunotia glacialis Meister			2/1		1/1
Eunotia implicata Nörpel, Lange-Bertalot et Alles			89/5	3/1	32/4
Eunotia incisa Gregory	Some individuals resembled *E. boreoalpina* Lange-Bertalot et Nörpel-Schempp.		2/2		400/9
Eunotia cf *inflata* (Grunow) Nörpel-Schempp et Lange-Bertalot		1/1	5/4	3/1	26/3

Species		Col1	Col2	Col3	Col4
Eunotia minor (Kützing) Grunow in Van Heurck			64/5	8/2	1/1
Eunotia monodon C.G. Ehrenberg					3/2
Eunotia nymanniana Grunow in Van Heurck					26/3
Eunotia paludosa Grunow				3/2	141/9
Eunotia soleirolii (Kützing) Rabenhorst					7/2
Eunotia sp. 1			1/1		
Eunotia sp. 2		1/1			
Eunotia steineckei Petersen			186/6	337/3	43/8
Eunotia tetraodon Ehrenberg			1/1		3/3
Fallacia insociabilis (Krasske) D.G. Mann		4/2	2/1		
Fragilaria acus (Kützing) Lange-Bertalot		1/1			
Fragilaria capucina Desmaziéres			8/4		1/1
Fragilaria gracilis Østrup			5/1	3/1	31/1
Fragilaria sp.1			3/1		
Fragilaria sp.2				2/1	
Fragilaria sp.3		1/1			
Fragilaria sp.4					3/1
Fragilariforma virescens (Ralfs) D.M. Williams et Round					2/2
Frustulia crassinervia (Breb.) Lange-Bertalot et Krammer					67/8
Frustulia saxonica Rabenhorst		1/1			7/4
Frustulia sp. 1				1/1	
Frustulia vulgaris (Thwaites) De Toni		9/7	22/7		
Gomphonema angustatum agg.	including *G. micropus* Kützing and *G. productum* (Grunow) Lange-Bertalot et Reichardt	185/14	114/12	11/2	
Gomphonema angustum Agardh		188/11			
Gomphonema clavatum agg.	including *Gomphonema clavatum* Ehrenberg, *G. montanum* Schuman and *G. subclavatum* Grunow	15/5	55/11	3/2	6/2
Gomphonema gracile Ehrenberg	Some individuals resembled *G. acidoclinatum* Lange-Bertalot et Reichardt and *G. hebridense* Gregory	52/7	52/7	10/3	28/6
Gomphonema lagerheimii A.Cleve			1/1		
Gomphonema parvulum (Kützing) Kützing		168/10	76/12	12/3	11/4
Gomphonema sp. 1				1/1	
Gomphonema sp. 2					1/1
Gomphonema tergestinum Fricke	There occurred intermediary morphotypes resembling *Reimeria sinuata*.	5/4			
Gyrosigma attenuatum (Kützing) Rabenhorst		2/1			

Species	Notes				
Hantzschia amphioxys (Ehr.) Grunow in Cleve et Grunow		8/4	13/4		
Hippodonta capitata (Ehr.) Lange-Bert., Metzeltin et Witkowski		1/1			
Kobayasiella cf *micropunctata* (Germain) Lange-Bertalot		23/4	90/6	65/3	387/6
Meridon circulare agg.	including *Meridon circulare* (Greville) Agardh and *Meridion constrictum* Ralfs	15/6	286/10	23/3	
Navicula cryptocephala Kützing		38/8	109/11	8/2	
Navicula cryptotenella Lange-Bertalot		104/14	68/10	4/2	11/1
Naviculadicta digitulus (Hustedt) Lange-Bertalot				20/1	
Navicula lanceolata (Agardh) Ehrenberg	sensu Lange-Bertalot	4/1			
Navicula menisculus Schumann		13/4	3/1		
Navicula phyllepta Kützing		2/1			
Navicula pseudobryophila Hustedt		3/2			
Navicula pseudokotschyi Lange-Bertalot		3/2			
Navicula radiosa Kützing		2/1			
Navicula recens (Lange-Bertalot) Lange-Bertalot		1/1			
Navicula rhynchocephala Kützing	sensu Lange-Bertalot		6/3		
Navicula seibigiana Lange-Bertalot		29/4			
Navicula sp. 1			1/1		
Navicula sp. 2			1/1		
Navicula sp. 3		1/1			
Navicula sp. 4		2/1			
Navicula sp. 5		7/1			
Navicula sp. 6			6/1		
Navicula sp. 7					1/1
Navicula sp. 8				1/1	
Navicula sp. 9		1/1			
Navicula tridentula Krasske			8/3	2/2	
Navicula tripunctata (O.F.Müller) Bory					1/1
Navicula trivialis Lange-Bertalot		6/2			
Navicula veneta Kützing		8/3	2/2		
Neidium affine (Ehrenb.) Pfitzer var. *affine*		1/1			
Neidium binodeforme Krammer		8/5			
Neidium bisulcatum (Lagerstedt) Cleve					6/1
Neidium hercynicum A. Mayer					19/6
Neidium iridis (Ehrenberg) Cleve			4/2		
Neidium sp.1				1/1	
Nitzschia amphibia Grunow		44/7			
Nitzschia archibaldii Lange-Bertalot			85/1		
Nitzschia debilis Pantocsek		1/1			

		Col1	Col2	Col3	Col4
Nitzschia dissipata (Kützing) Grunow		37/5	2/1		
Nitzschia dubia W. Smith		27/1			
Nitzschia hantzschiana Rabenhorst		31/7	122/8	35/2	19/2
Nitzschia linearis (Agardh) W. Smith		253/13	189/7	1/1	
Nitzschia palea (Kützing) W.Smith		174/13	124/6	29/3	11/3
Nitzschia perminuta (Grunow) M.Peragallo			69/4		
Nitzschia semirobusta Lange-Bertalot		2/1			
Nitzschia sinuata (Thwaites) Grunow		3/2			
Nitzschia sp. 1		7/1			
Nupela sp. 1		1/1			
Nupela sp. 2			1/1		
Nupela sp. 3					3/1
Pinnularia appendiculata (Agardh) Cleve			19/5	1/1	19/5
Pinnularia borealis Ehrenberg		3/1	4/4	1/1	
Pinnularia brandeliformis Krammer			1/1		
Pinnularia divergens W. Smith		1/1			
Pinnularia major (Kützing) Rabenhorst					10/2
Pinnularia microstauron (C.G. Ehrenberg) P.T. Cleve		1/1	1/1		
*Pinnularia nodosa (*Ehrenberg) W.Smith			5/1		
Pinnularia obscura Krasske		6/4	6/3	1/1	
Pinnularia rupestris Hantzsch in Rabenhorst		5/2	9/2	1/1	1/1
Pinnularia sp. 1			4/1		
Pinnularia sp. 2		1/1			
Pinnularia sp. 3				2/1	
Pinnularia sp. 4			1/1		
Pinnularia sp. 5			4/1		
Pinnularia stomatophora (Grunow) Cleve			5/4	1/1	2/2
Pinnularia subcapitata Gregory	Some individuals resembled *P. sinistra* Krammer.		48/8	5/3	141/9
Pinnularia viridis agg.		15/8	37/11	3/1	65/6
Placoneis elginensis (Greg.) Cox		7/5	20/6		
Placoneis ignorata (Schimanski) Lange-Bertalot		2/2	23/6		
Planothidium lanceolatum agg.	including *P. lanceolatum* (Brébisson ex Kützing) Lange-Bertalot and *P. frequentissimum* (Lange-Bertalot) Lange-Bertalot	42/10	931/12	5/2	
Psammothidium subatomoides (Hustedt) Bukht. et Round		26/9	236/11	11/2	21/1
Psammothidium ventrale (Krasske) Bukht. et Round			1/1		

Species		A	B	C	D
Reimeria sinuata (Gregory) Kociolek et Stoermer		3/3	1/1		
Rhoicosphenia abbreviata (Agardh) Lange-Bertalot		1/1			
Rhopalodia gibba (Ehrenberg) O.Müller var. *gibba*		22/3			
Rossithidium petersenii (Hustedt) F.E. Round et Bukhtiyarova			1/1	24/1	
Sellaphora pupula (Kützing) Mereschkowksy		12/6	19/6	2/1	
Stauroneis acuta W. Smith		4/1	1/1		
Stauroneis anceps Ehrenberg		5/3	6/2	1/1	
Stauroneis gracillima Hustedt			4/2		
Stauroneis kriegeri Patrick			1/1		
Stauroneis smithii Grunow		16/8		1/1	
Stauroneis cf *subgracilis* Lange-Bertalot et Krammer		2/1	12/4		
Stauroneis tackei (Hustedt) Krammer et Lange-Bertalot		3/1			
Staurosira mutabilis (W. Smith) Grunow			124/2		
Stenopterobia delicatissima (Lewis) Brebisson ex Van Heurck					19/3
Surirella angusta Kützing		17/5	12/3		
Surirella brebissonii Krammer et Lange-Bertalot		27/11	2/2		
Surirella helvetica Brun		5/1			
Surirella linearis W.M.Smith		1/1			
Surirella cf *minuta* Brebisson		3/2	1/1		
Surirella spiralis Kützing		6/3			
Surirella tenera Gregory			13/3		
Synedrella parasitica (W. Smith) Round et Maidana		2/1			
Tabellaria fenestrata (Lyngbye) Kützing				2/1	19/1
Tabellaria flocculosa agg.	including *Tabellaria flocculosa* (Roth) Kützing and *Tabellaria ventricosa* Kützing	1/1	4/2	3/1	170/7
Ulnaria ulna (Nitzsch) Compère			7/4		2/1