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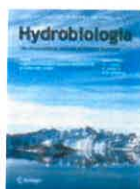
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## Subfossil diatoms and chironomids along an altitudinal gradient in the High Tatra Mountain lakes: a multi-proxy record of past environmental trends

Peter Bitušík · Vladimír Kubovčík ·  
Elena Štefková · Peter G. Appleby ·  
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**Abstract** Multi-proxy approach was used to reconstruct the environmental conditions of remote lakes in the High Tatra Mountains (Slovakia) over the past few centuries (approximately 500–1000 years). Short sediment cores (~30 cm) taken from three morphologically similar glacial lakes distributed along altitudinal gradient (subalpine to alpine conditions) were analysed for organic matter content (LOI), diatoms and

chironomids. Both descriptive and correlative approaches were used for analysing stratigraphical data. Predictive canonical correspondence analysis and co-correspondence analysis were applied to directly relate physical and biological proxies to each other. The relationship between LOI and biotic proxies was inconsistent across groups and lakes. Concordant patterns in diatom and chironomid composition were found in two non-acidified lakes. Common trends in those assemblages indicated major past environmental events such as the Little Ice Age, air pollution and lake acidification. In contrast, no relationship between the composition of diatom and chironomid assemblages was found in the formerly acidified lake, suggesting different responses of assemblages to acidification. While chironomids showed shifts that are attributable to recovery, diatoms assemblage remained relatively stable throughout the uppermost layers of the sediment record. On the other hand, climatic-driven changes in assemblages detected in the deeper layers were more pronounced in diatoms than in chironomids.

Guest editors: K. Buczkó, J. Korponai, J. Padišák & S. W. Starratt  
Palaeolimnological Proxies as Tools of Environmental Reconstruction in Fresh Water

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Co-correspondence analysis

### Introduction

Intensive study of remote alpine and arctic lakes in the past few decades has revealed an extremely high

sensitivity of these lakes to global effects such as atmospheric pollution and climatic change, as well as minor changes of regional importance (Rouse et al., 1997). Relatively subtle, short-term variability in air temperature is extremely well mirrored in epilimnion lake water temperature (Livingstone & Lotter, 1998). The complex effects of long-term climatic trends, regardless of whether natural or human induced, are potentially recorded in lake sediments, and lake sediments can thus be used as a means of reconstructing past climate over long time-scales. However, the usefulness of this approach depends on the sensitivity and accuracy of the various proxies and the extent to which the climate signal in the sediment record is obscured by noise from other influences (Battarbee et al., 2002b). Past climatic changes can be tracked by assemblages of aquatic organisms such as diatoms and chironomids that may be more sensitive indicators of climatic changes than terrestrial groups (Smol et al., 1991). They can be affected by climatic variability directly through their life cycles (Davidson, 1991; Smol et al., 1991) and indirectly through processes such as stratification, water quality and habitat changes (Anderson et al., 1996; Gaedke et al., 1998; Walker, 2001; Weckström & Korhola, 2001). Due to this sensitivity, diatoms and chironomids are used quite extensively as proxy indicators of climatic changes (e.g., Anderson, 2000; Brooks & Birks, 2004).

Lakes of glacial origin in the Tatra Mountains, situated at the Slovak-Polish border, became the focus of multidisciplinary research within the EU-funded projects AL:PE, MOLAR and EMERGE. Palaeolimnological analyses were employed to document the long-term effects of acidification in the lake communities (Cameron et al., 1999; Stuchlík et al., 2002; Clarke et al., 2005; Kubovčík & Bitušík, 2006) and to reconstruct climate patterns over the last 200 years, comparing the palaeolimnological evidence with instrumental climate data (Šporka et al., 2002). However, comparisons between various aquatic assemblages as climate proxies and instrumental climate records during the past 200 years did not show clear-cut results over a range of European mountain lakes (Battarbee et al., 2002a).

Specifically, in the Tatra Mountains, a relatively strong correlation was found between diatom species composition and reconstructed summer air temperature in Nižné Terianske pleso. In spite of decadal-scale temperature fluctuations at this lake (Agustí-Panareda &

Thompson, 2002), the response of chironomids was weak (Šporka et al., 2002). An equivocal reaction of diatoms and chironomids to climatic change was observed in other alpine lakes, too (e.g., Koinig et al., 2002). In contrast, those data overall indicated that organic matter content of sediments may be a good indicator of varying mean annual temperature in lakes, especially in soft water systems where the sources of organic matter are mainly autochthonous (Battarbee et al., 2002a).

Shared responses are ecologically interesting because they suggest that taxonomically divergent groups are controlled by relatively few environmental factors (Paavola et al., 2003). Similar structures between different groups, however, may be a consequence of biotic interactions among trophic levels (e.g., Jackson & Harvey, 1993). In a bottom-up approach of biodiversity, plant species composition will first affect the herbivores that directly depend on these plants, which will in turn affect higher trophic levels (Schaffers et al., 2008). Therefore, when dealing with a range of taxonomic groups that have different trophic levels and positions in the food web, one should bear in mind various indirect ways of climatic influences and possible complex interactions (Battarbee et al., 2002a).

By examining the degree of synchronicity of the responses among biostratigraphic indicators, it is possible to assess which proxy indicator(s) has responded most sensitively to subtle Holocene environmental changes. Only few palaeolimnological studies have tackled this subject (Fallu et al., 2005). To our knowledge, no studies have explicitly tested for shared structures between subfossil assemblages.

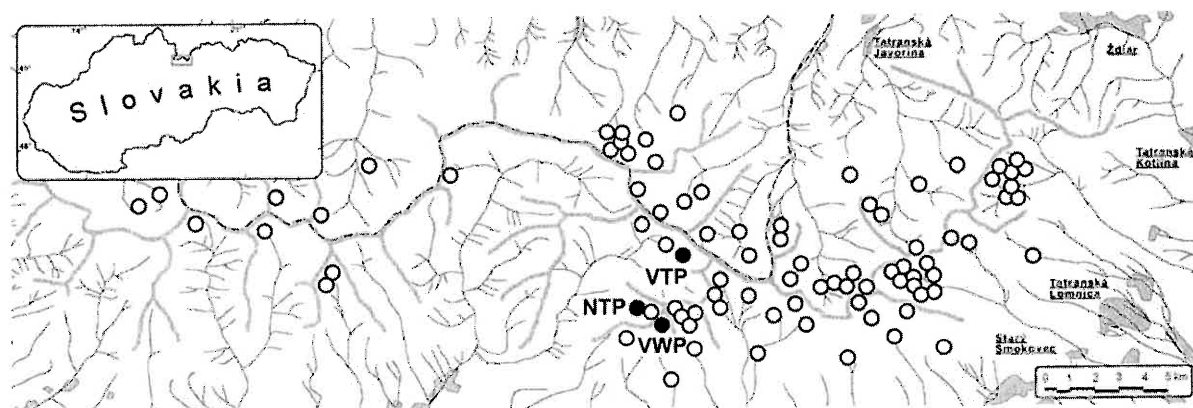
The motivation for this study was to provide analyses of the deeper parts of sediment cores that have not yet been studied, taken from three Tatra Mountain lakes situated at different altitudes. The primary aim of this study was to discern to what extent the sediment records from these lakes could reflect environmental changes through time within the region. Our approach has been to make comparisons between the organic matter content as a useful temperature proxy and the composition of diatom and chironomid assemblages. In conjunction with this, the sensitivity and usefulness of subfossil diatoms and chironomids used as proxy indicators were evaluated. Subsequently, the relationships between assemblages of different trophic levels were directly evaluated and compared with those provided by organic matter.

### Study sites

The three lakes of glacial origin are located in the High Tatra Mountains in northern Slovakia. The mountain range is characterised by steep changes in temperature and precipitation along an altitudinal gradient. The average annual air temperature decreases with elevation by 0.6°C per 100 m, being 1.6 and −3.8°C at elevations of 1,778 and 2,635 m, respectively (Konček & Orlicz, 1974). The amount of precipitation varies from ~1.0 to ~1.6 m y<sup>−1</sup> between 1,330 and 2,635 m a.s.l., but reaches >2.00 m y<sup>−1</sup> in some valleys (Chomitz & Šamaj, 1974). Snow cover usually lasts from October to June at elevations >2,000 m.

The surveyed lakes are situated above the present-day timberline and span elevations from 1,725 to 2,157 m a.s.l. (Fig. 1). Bedrock in the study area consists mainly of granitoids (biotite granodiorites to tonalites). Soils are dominated by undeveloped podzols, leptosols and regosols. The dominant vegetation of lake catchments changes from subalpine bushes with dwarf pine (*Pinus mugo*) to alpine meadows (dry tundra) with increasing percentage of rocks. The lake basins are relatively deep with small surface areas. All lakes are soft water, oligotrophic and fishless. Further details on some environmental characteristics can be found in Table 1.

The lakes encompass a gradient of climate and catchment characteristics (soil and vegetation



**Fig. 1** Location of the most important Tatra Mountains lakes (circles). Study lakes are denoted by black circles and assigned as follows: VTP—Vyšné Temnosmrečinské pleso, NTP—Nižné Terianske pleso and VWP—Vyšné Wahlenbergovo pleso

**Table 1** Locations and environmental characteristics of the study lakes

Characteristic/lake name	Vyšné Temnosmrečinské pleso	Nižné Terianske pleso	Vyšné Wahlenbergovo pleso
Latitude (N)	49°11'20"	49°10'11"	49°09'51"
Longitude (E)	20° 02'22"	20°00'51"	20°01'37"
Altitude (m a.s.l.)	1725	1940	2157
Lake area (ha)	5.56	5.56	5.17
Maximum depth (m)	20	47.3	20.6
Catchment area (ha)	112	110	32
Max. mean LSTW in 2001 (°C)	12.9	11.8	11.6
Ice-cover duration (days)	155	203	217
Catchment rocks/screes/alpine meadows (%)	40/34/26	40/32/28	37/51/12
Surface inflow/outflow	+/+	+/-	-/-

Explanations: data on altitude, area and maximum depth of lakes come from Gregor & Pacl (2005), data on LSTW (lake surface water temperature) from Šporka et al. (2006)

coverage). They span a gradient of human impacts, as well, since the negative effects of acid deposition on the lakes in the second half of the twentieth century increased with altitude (Kopáček & Stuchlík, 1994). Recently, there are no direct human activities occurring in the lake catchments. All kinds of land use have been prohibited since the 1950s when the Tatra Mountains became a national park.

## Methods

Lake sediment cores were taken in August 1996 and in April 2001 using a modified Kajak corer from the deepest parts of the lakes. The cores were sectioned in the field into 0.5-cm thick layers except for Nižné Terianske pleso, which was divided into 0.2-cm slices. The samples were stored in plastic bags and kept at 4°C for later analysis.

The organic matter content (%) in the sediment cores was measured through loss-on-ignition (LOI) when dried sediment was combusted in a muffle furnace at 550°C for 2 h. The analyses were performed at the Faculty of Sciences, Charles University in Prague.

The upper parts of the cores, representing the past ca. 200 years, were analysed for  $^{210}\text{Pb}$ ,  $^{226}\text{Ra}$ ,  $^{137}\text{Cs}$  and  $^{241}\text{Am}$  by direct gamma assay using Ortec HPGe GWL series well-type coaxial low background intrinsic germanium detectors (see Appleby & Piliposian (2006) for more details). Radiometric dates were calculated from the  $^{210}\text{Pb}$  and  $^{137}\text{Cs}$  records using the procedures described in Appleby (2001). Dating of deeper sediment samples was estimated applying a mean sedimentation rate. A summary of all cores is given in Table 2.

Sediment samples for diatom analysis were treated through the standard procedures (Battarbee, 1986) using  $\text{H}_2\text{O}_2$  and HCl and repeated washing in distilled water. Diatom samples were then mounted on slides in Naphrax. At least 400 diatom valves were counted using a LEICA DMLB microscope with 100× oil immersion and phase contrast objectives. Identification, taxonomy and basic information on ecological preferences of the diatom taxa followed Krammer & Lange-Bertalot (1986, 1988, 1991a, b), Lange-Bertalot & Krammer (1989), Charles (1985), van Dam et al. (1994), Tolotti (2001), and Schmidt et al. (2004).

Sediment samples for analysis of chironomid remains were sieved using a 233- and then a 85- $\mu\text{m}$  sieve, respectively (Walker & Paterson, 1985). The fractions retained on the sieves were manually sorted at 7–40× magnifications in a counting tray. After separation, the sediments were dried at 120°C to constant weight to allow the calculation of head capsule concentrations per gram of the dry sediment, except for the sediments from Nižné Terianske pleso, where the number of chironomid remains was expressed per 10 cm<sup>3</sup> of wet sediment.

Chironomid head capsules were mounted, ventral side up, in Berlese solution on microscopic slides. For identification, the Wiederholm (1983), Kowalyk (1985), Schmid (1993) and Ekrem (2004) keys were used. The nomenclature of Chironomidae follows that of Sæther & Spies (2004). In order to achieve more reliable taxonomic results, larvae and pupae collected from the investigated lakes during the past two decades were compared with those in the subfossil material. Remains consisting of the right half of the head capsule or more than half of the mentum were enumerated as a whole head capsule.

**Table 2** Details on the cores studied: coring, subsampling and dating

Lake name	Core code	Coring date	Length (cm)	Sampling interval (cm)	Period covered (AD)	Studied period (years)
Vyšné Temnosmrečinské pleso	TE-1	April 2001	30	0.5	2001–1828 ± 37 1828–1044 ± 207	957 ± 207
Nižné Terianske pleso	TERI96/5 (chironomids) TERI96/7 (diatoms)	August 1996	30.4	0.2	1996–1784 ± 18	156 ± 17
Vyšné Wahlenbergovo pleso	FU-1	April 2001	19	0.5	2001–1862 ± 39 1862–1624 ± 105	377 ± 105

Estimated ages are indicated by italics

Fragments that consisted of the left half or of less than half of the mentum were excluded.

Diatom and chironomid stratigraphic diagrams were produced using TILIA 2.0.b.4 and TGView 2.0.2 computer software (Grimm, 2004). Biostratigraphical zones were detected according to the major changes in composition of assemblages using constrained incremental sum of squares cluster analysis (CONISS, Grimm, 1987). Diatom and chironomid data were square root transformed for cluster analysis. All the taxa were included in the analysis.

For the purpose of ordination analyses, data on assemblage composition were summarised in the incidence (presence/absence) and abundance matrices for each taxonomic group (diatoms, chironomids) and lake. Both kinds of composition matrices were used in the analyses because each can provide different but complementary information (Heino, 2008). Species with less than five specimens were deleted from the original data matrices to improve the signal-to-noise ratio (Gauch, 1982). Altogether, 12 site-by-species matrices were constructed (two groups  $\times$  two matrices  $\times$  three lakes). The chironomid incidence matrix of Vyšné Wahlenbergovo pleso was excluded from the subsequent analyses due to a lack of variability (matrix of ones). Ordination methods were used to examine the relationships between organic matter and ecological assemblages and between individual assemblages.

The diatom and chironomid composition matrices were subjected to preliminary indirect ordination analysis. Detrended correspondence analysis (Hill & Gauch, 1980) with detrending by segments was used to determine whether linear- or unimodal-based ordination techniques were more appropriate for the data. A majority of the analyses yielded gradient lengths from 1.6 to 2.2 standard deviations. The features of the data suggested that both linear- and unimodal-based techniques may be appropriate (ter Braak and Prentice, 1988). However, the qualitative nature of incidence matrices and the predefined total abundance of diatoms per layer make unimodal techniques more appropriate (ter Braak & Schaffers, 2004). Thus, methods related to correspondence analysis were applied to all the composition matrices, facilitating comparability of the results across different datasets.

Canonical correspondence analysis (CCA) was used to assess the relationship between the organic

matter content of sediments as a good temperature indicator (Battarbee et al., 2002b) and composition of diatom and chironomid assemblages, respectively. Predictive CCA (ter Braak & Schaffers, 2004) was applied rather than the usual exploratory version of this analysis, which enabled a direct comparison of the results with those of predictive co-correspondence analysis (CoCA; see below). Predictive CCA uses a 'leave-one-out' procedure to validate the models. This means, in our case, that an analysis was carried out as many times as there were layers, each time with a different layer left out and applying the obtained model to the omitted layer to predict its species composition from the organic matter content. Predicted taxonomic composition was compared to the observed composition on the basis of sum of squared prediction errors ( $ssp_a$ ). The prediction accuracy of each model was assessed using the cross-validated fit, calculated as  $100 \times (1 - ssp_a / ssp_0)$ , where  $ssp_0$  is the sum of squared prediction errors under the null model of no relationship. Unlike explained variation in explanatory CCA, cross-validated fit can be negative when the model fit is so poor that the null model predicts the data better. Any fit above zero, however, indicates that prediction is better than could have been expected by chance, implicitly validating the model without additional statistical tests (Schaffers et al., 2008).

The relationships between diatom and chironomid assemblages of different lakes were assessed using CoCA (ter Braak & Schaffers, 2004). This direct ordination method relates one community dataset to another by maximising the weighted covariance between the weighted averaged species scores of the communities. The CoCA attempts to identify the patterns (ecological gradients) that are common to both assemblages. Both a symmetric descriptive and an asymmetric predictive form have been developed. Predictive CoCA provides a way to use the diatom assemblage as a predictor of the chironomid assemblage and to assess the predictive value of models via a cross-validation procedure (see above). The use of the same cross-validated fit measure in predictive CCA and predictive CoCA allowed a direct comparison of the ability of different predictors (diatom incidence matrix, diatom abundance matrix and organic matter content) to predict the composition of chironomid assemblages (defined in terms of incidence or abundance).

Schaffers et al. (2008) pointed out that the predictive models themselves are validated implicitly (when the cross-validated fit is above zero), but there is still a need to judge whether differences between models (using different predictors) are actually significant or could just as well be attributed to random variation. The predictive power of different models was compared using a two-sided simple randomisation test (van der Voet, 1994). The difference in mean square of prediction errors (T) of the compared models was used as a test statistic. The significance of difference between models was obtained by a comparison of the observed T statistic with a distribution of this statistic generated by randomised data (999 random rearrangements of site prediction errors).

## Results

### Dating

The  $^{210}\text{Pb}$  results from the Vyšné Temnosmrečinské pleso core TA0019 suggested a slow and relatively uniform sedimentation rate of  $0.0064 \text{ g cm}^{-2} \text{ yr}^{-1}$  ( $0.058 \text{ cm yr}^{-1}$ ) during the past 150 years or so. Since this value is typical of remote undisturbed sites, it is not unreasonable to suppose that this rate has persisted over a much longer timescale. Table 3 gives dates calculated on this basis.

Results of an extrapolated chronology for the Nižné Terianske pleso core TERI96/7, down to a depth of 6 cm (dated 1784), are given in Appleby (2000). The presence of a number of layers of dense sediment at depths varying from 2 to 29 cm suggests that sedimentation rates at this site are likely to have been quite variable, with several episodes of rapid accumulation. In view of this, any further extrapolation is likely to be very unreliable unless supported by well-defined correlations with cores from more stable sites.

Due to the very slow accumulation rate in the Vyšné Wahlenbergovo pleso core FU-1,  $^{210}\text{Pb}/^{226}\text{Ra}$  equilibrium being reached at a depth of just 6 cm, there were only two  $^{210}\text{Pb}$  data points above the  $^{210}\text{Pb}/^{226}\text{Ra}$  equilibrium depth. However, the results did suggest a mean sedimentation rate of  $0.0057 \text{ g cm}^{-2} \text{ yr}^{-1}$  ( $0.043 \text{ cm yr}^{-1}$ ), a value typical of remote undisturbed sites. In the absence of evidence of earlier disturbances, it would therefore

**Table 3** Extrapolated  $^{210}\text{Pb}$  chronology of Vyšné Temnosmrečinské pleso core TA0019

Depth		Chronology			Sedimentation rate		
cm	$\text{g cm}^{-2}$	Date	Age		$\text{g cm}^{-2} \text{ yr}^{-1}$	$\text{cm yr}^{-1}$	$\pm (\%)$
		AD	y	$\pm$			
0.00	0.00	2001	0				
0.25	0.01	1999	2	0	0.0064	0.11	21.5
0.75	0.04	1994	7	1	0.0064	0.09	21.5
1.25	0.08	1988	13	3	0.0064	0.07	21.5
1.75	0.13	1981	20	4	0.0064	0.07	21.5
2.25	0.17	1974	27	6	0.0064	0.07	21.5
2.75	0.22	1967	34	7	0.0064	0.07	21.5
3.25	0.27	1959	42	9	0.0064	0.07	21.5
3.75	0.32	1952	49	11	0.0064	0.06	21.5
4.25	0.37	1944	57	12	0.0064	0.06	21.5
4.75	0.42	1936	65	14	0.0064	0.06	21.5
5.25	0.47	1927	74	16	0.0064	0.06	21.5
5.75	0.53	1919	82	18	0.0064	0.05	21.5
6.25	0.59	1909	92	20	0.0064	0.05	21.5
6.75	0.65	1899	102	22	0.0064	0.05	21.5
7.25	0.71	1890	111	24	0.0064	0.05	21.5
7.75	0.77	1880	121	26	0.0064	0.05	21.5
8.25	0.84	1871	130	28	0.0064	0.05	21.5
8.75	0.90	1860	141	30	0.0064	0.04	21.5
9.25	0.98	1848	153	33	0.0064	0.04	21.5
9.75	1.07	1835	166	36	0.0064	0.04	21.5
10.25	1.15	1821	180	39	0.0064	0.04	21.5
10.75	1.24	1808	193	41	0.0064	0.04	21.5
11.25	1.33	1794	207	45	0.0064	0.03	21.5
11.75	1.44	1777	224	48	0.0064	0.03	21.5
12.25	1.54	1760	241	52	0.0064	0.03	21.5
12.75	1.65	1744	257	55	0.0064	0.03	21.5
13.25	1.74	1729	272	59	0.0064	0.03	21.5
13.75	1.86	1711	290	62	0.0064	0.02	21.5
14.25	2.01	1687	314	68	0.0064	0.02	21.5
14.75	2.15	1665	336	72	0.0064	0.02	21.5
15.25	2.29	1644	357	77	0.0064	0.02	21.5
15.75	2.43	1622	379	82	0.0064	0.02	21.5
16.25	2.55	1604	397	85	0.0064	0.03	21.5
16.75	2.69	1582	419	90	0.0064	0.02	21.5
17.25	2.88	1552	449	97	0.0064	0.01	21.5
17.75	3.11	1515	486	105	0.0064	0.02	21.5
18.25	3.28	1489	512	110	0.0064	0.02	21.5
18.75	3.38	1474	527	113	0.0064	0.03	21.5
19.25	3.52	1451	550	118	0.0064	0.02	21.5
19.75	3.69	1425	576	124	0.0064	0.02	21.5

**Table 3** continued

Depth cm	g cm <sup>-2</sup>	Chronology			Sedimentation rate		
		Date	Age		g cm <sup>-2</sup> y <sup>-1</sup>	cm y <sup>-1</sup>	± (%)
		AD	y	±			
20.25	3.83	1403	598	129	0.0064	0.03	21.5
20.75	3.95	1385	616	133	0.0064	0.03	21.5
21.25	4.08	1365	636	137	0.0064	0.02	21.5
21.75	4.26	1337	664	143	0.0064	0.02	21.5
22.25	4.42	1311	690	149	0.0064	0.02	21.5
22.75	4.57	1288	713	153	0.0064	0.02	21.5
23.25	4.76	1259	742	160	0.0064	0.02	21.5
23.75	4.96	1227	774	167	0.0064	0.02	21.5
24.25	5.12	1203	798	172	0.0064	0.02	21.5
24.75	5.23	1186	815	176	0.0064	0.03	21.5
25.25	5.32	1171	830	179	0.0064	0.03	21.5
25.75	5.41	1157	844	182	0.0064	0.03	21.5
26.25	5.50	1143	858	185	0.0064	0.04	21.5
26.75	5.59	1129	872	188	0.0064	0.04	21.5
27.25	5.68	1115	886	191	0.0064	0.03	21.5
27.75	5.77	1100	901	194	0.0064	0.03	21.5
28.25	5.87	1085	916	197	0.0064	0.03	21.5
28.75	5.98	1069	932	201	0.0064	0.03	21.5
29.25	6.10	1050	951	205	0.0064	0.03	21.5

NB: Dates in italics (for sediments below 14 cm) should be regarded with more caution due to high irregular variations in values of dry bulk density

seem reasonable to suppose that sedimentation rates have been stable over a much longer period than that covered by the <sup>210</sup>Pb time span. Table 4 gives dates calculated on this basis.

#### Biostratigraphies

##### *Vyšné Temnosmrečinské pleso*

**Diatoms** A total of 100 diatom taxa were recorded, most of them benthic. Fourteen species occurred at a minimum of over 5%. Of these, three species achieved abundance higher than 30% (*Fragilaria construens* f. *venter*, *F. pinnata* and *F. pseudoconstruens*).

Based on changes in the assemblage composition, four zones can be detected (Fig. 2). Zone DTE-I (depth 30–10 cm) is dominated by *Fragilaria* species at relative abundance amounting to 81% at the 28 cm depth, except for at 14 cm where they reach only 40%. Also, *Achnanthes* species (7–17%) significantly

**Table 4** Extrapolated <sup>210</sup>Pb chronology of Vyšné Wahlenbergovo pleso core FU-1

Depth cm	g cm <sup>-2</sup>	Chronology			Sedimentation rate		
		Date	Age		g cm <sup>-2</sup> y <sup>-1</sup>	cm y <sup>-1</sup>	± (%)
		AD	y	±			
0.00	0.00	2001	0				
0.25	0.02	1997	4	1	0.0057	0.05	28.1
0.75	0.08	1987	14	4	0.0057	0.04	28.1
1.25	0.16	1974	27	8	0.0057	0.04	28.1
1.75	0.23	1960	41	12	0.0057	0.04	28.1
2.25	0.30	1948	53	15	0.0057	0.04	28.1
2.75	0.37	1936	65	18	0.0057	0.04	28.1
3.25	0.44	1924	77	22	0.0057	0.04	28.1
3.75	0.50	1913	88	25	0.0057	0.04	28.1
4.25	0.57	1901	100	28	0.0057	0.04	28.1
4.75	0.64	1889	112	31	0.0057	0.04	28.1
5.25	0.70	1878	123	35	0.0057	0.05	28.1
5.75	0.76	1867	134	38	0.0057	0.05	28.1
6.25	0.81	1858	143	40	0.0057	0.06	28.1
6.75	0.86	1850	151	42	0.0057	0.06	28.1
7.25	0.91	1841	160	45	0.0057	0.06	28.1
7.75	0.96	1832	169	47	0.0057	0.05	28.1
8.25	1.02	1823	178	50	0.0057	0.05	28.1
8.75	1.07	1813	188	53	0.0057	0.05	28.1
9.25	1.12	1804	197	55	0.0057	0.06	28.1
9.75	1.17	1796	205	58	0.0057	0.06	28.1
10.25	1.22	1786	215	60	0.0057	0.05	28.1
10.75	1.28	1777	224	63	0.0057	0.05	28.1
11.25	1.33	1768	233	65	0.0057	0.06	28.1
11.75	1.38	1759	242	68	0.0057	0.05	28.1
12.25	1.44	1749	252	71	0.0057	0.05	28.1
12.75	1.49	1739	262	73	0.0057	0.05	28.1
13.25	1.54	1730	271	76	0.0057	0.06	28.1
13.75	1.59	1722	279	78	0.0057	0.06	28.1
14.25	1.64	1713	288	81	0.0057	0.06	28.1
14.75	1.69	1704	297	83	0.0057	0.06	28.1
15.25	1.74	1695	306	86	0.0057	0.06	28.1
15.75	1.79	1687	314	88	0.0057	0.05	28.1
16.25	1.85	1677	324	91	0.0057	0.05	28.1
16.75	1.90	1667	334	94	0.0057	0.05	28.1
17.25	1.96	1657	344	97	0.0057	0.05	28.1
17.75	2.01	1648	353	99	0.0057	0.05	28.1
18.25	2.07	1639	362	102	0.0057	0.05	28.1
18.75	2.12	1629	372	104	0.0057	0.05	28.1
19.25	2.17	1620	381	107	0.0057	0.05	28.1
19.75	2.22	1611	390	110	0.0057	0.06	28.1

Table 4 continued

Depth cm	g cm <sup>-2</sup>	Chronology			Sedimentation rate		
		Date	Age		g cm <sup>-2</sup> y <sup>-1</sup>	cm y <sup>-1</sup>	± (%)
		AD	y	±			
20.25	2.28	1602	399	112	0.0057	0.06	28.1
20.75	2.32	1593	408	114	0.0057	0.06	28.1
21.25	2.37	1585	416	117	0.0057	0.06	28.1
21.75	2.42	1576	425	119	0.0057	0.06	28.1
22.25	2.47	1568	433	122	0.0057	0.06	28.1
22.75	2.52	1560	441	124	0.0057	0.06	28.1
23.25	2.57	1551	450	126	0.0057	0.06	28.1
23.75	2.62	1542	459	129	0.0057	0.06	28.1
24.25	2.67	1532	469	132	0.0057	0.05	28.1
24.75	2.73	1522	479	135	0.0057	0.04	28.1
25.25	2.80	1510	491	138	0.0057	0.04	28.1
25.75	2.86	1499	502	141	0.0057	0.05	28.1
26.25	2.91	1490	511	144	0.0057	0.05	28.1
26.75	2.97	1481	520	146	0.0057	0.05	28.1
27.25	3.02	1471	530	149	0.0057	0.05	28.1
27.75	3.08	1461	540	152	0.0057	0.05	28.1
28.25	3.13	1451	550	154	0.0057	0.05	28.1
28.75	3.19	1441	560	157	0.0057	0.05	28.1
29.25	3.26	1430	571	160	0.0057	0.05	28.1
29.75	3.32	1419	582	163	0.0057	0.04	28.1
30.25	3.38	1409	592	166	0.0057	0.05	28.1
30.75	3.44	1398	603	169	0.0057	0.05	28.1
31.25	3.50	1387	614	172	0.0057	0.04	28.1
31.75	3.56	1376	625	175	0.0057	0.05	28.1
32.25	3.62	1366	635	178	0.0057	0.05	28.1
32.75	3.69	1353	648	182	0.0057	0.04	28.1
33.25	3.77	1340	661	185	0.0057	0.04	28.1
33.75	3.83	1328	673	189	0.0057	0.04	28.1
34.25	3.91	1316	685	192	0.0057	0.04	28.1

contribute to this assemblage. *Cymbella minuta*, *Denticula tenuis*, *Navicula minuscula* and *Nitzschia paleacea* make up a stable part of the assemblage through this zone, with a relative abundance <8% whilst *Navicula minuscula* increases in the uppermost samples of the zone. In Zone DTE-II (10–7 cm), *Fragilaria* species, mainly *F. pinnata* (25–41%) and *F. pseudoconstruens* (22–28%), remain as dominant elements. *F. brevistriata*, *F. construens* f. *construens* show an increase in proportion of the assemblage. *Cyclotella stelligera* reaches its greatest proportion in the bottom of this zone. Zone DTE-III (7–4 cm) is characterised

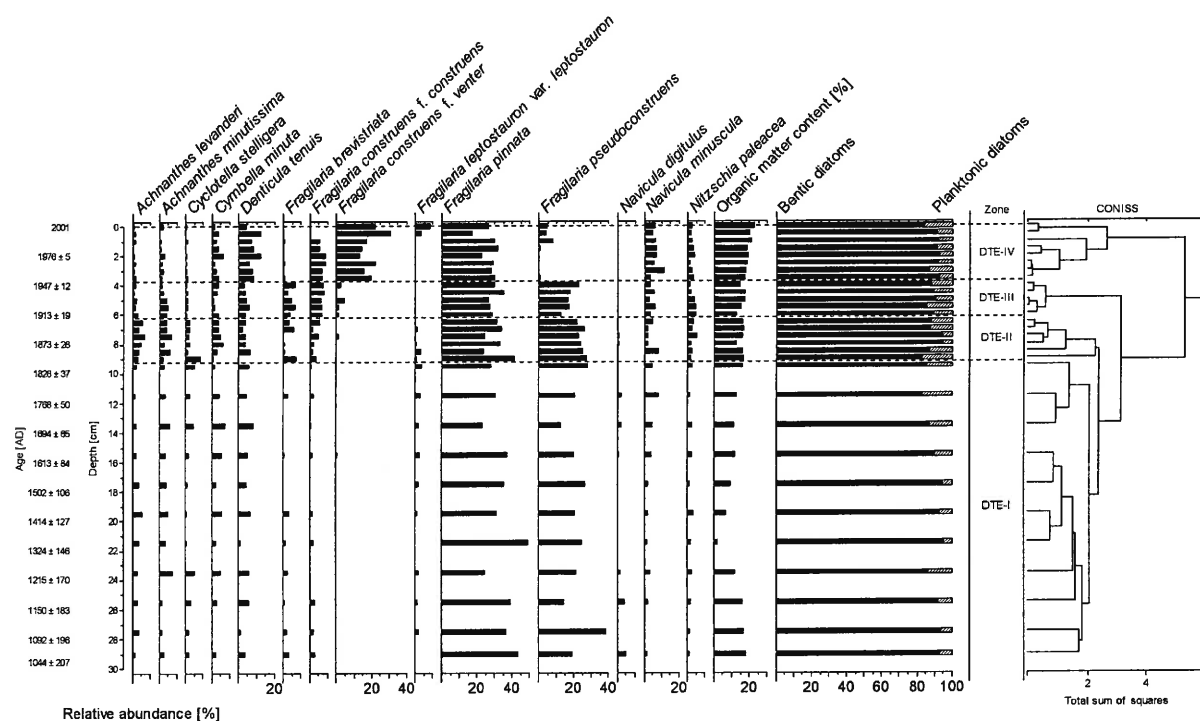
by a slight decrease of *Fragilaria pseudoconstruens* and *Achnanthes* species, while an increase in the relative abundance of *F. brevistriata* and *F. construens* f. *construens* is evident. Zone DTE-IV (4–0 cm) is dominated by *F. construens* f. *venter* and *F. pinnata*, and *F. construens* f. *construens*, *F. brevistriata*, and *F. pseudoconstruens* disappear, but the second species reappears again from 1.5 cm. Other *Fragilaria* species persist as a minor element of the assemblage. In conjunction with this trend, slight increase in *Navicula minuscula* occurs and *Denticula tenuis* reaches significant proportion (up to 12%).

**Chironomids** In total, 14,025 chironomid head capsules from 15 taxa were analysed. Subfossil chironomid density varied from 6 to 354 specimens g<sup>-1</sup> dry sediment. The *Tanytarsus lugens* group (57.8%) and *Micropsectra* spp. (33.7%) made up 91% of the chironomid assemblages. The other taxa that achieved an average abundance of more than 1% were *Procladius* (*Holotanypus*) sp. (5.5%) and *Heterotrissocladius marcidus* (1.1%).

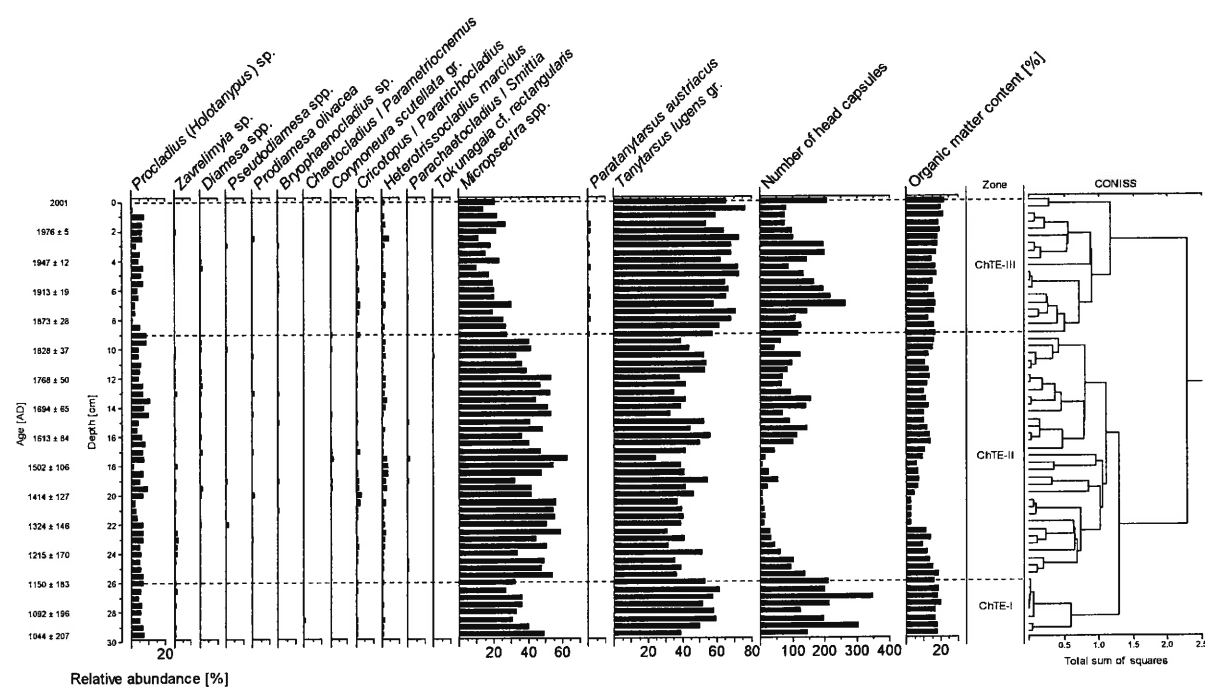
Changes in the chironomid record can be divided into three zones (Fig. 3). The oldest sediments of Zone ChTE-I (30–26 cm) are characterised by a high number of chironomid remains and dominance of the *Tanytarsus lugens* group. Opposite trends in the relative abundance of both taxa show a marked transition from Zone ChTE-I to Zone ChTE-II. The beginning of Zone ChTE-II (26–9 cm), especially between 24 and 17.5 cm, is defined by a significant reduction in the head capsule density. *Micropsectra* spp. remains a dominant taxon but declines in relative abundance, while the importance of the *Tanytarsus lugens* group starts to increase in the uppermost samples of the zone. *Heterotrissocladius marcidus*, *Diamesa* spp. and *Zavreliomyia* sp. reach their greatest proportions in this interval. In Zone ChTE-III (9–0 cm), the *T. lugens* group becomes dominant, while *Micropsectra* spp. gradually decreases in the most recent sediments, and *Paratanytarsus austriacus* first appears. *Procladius* (*Holotanypus*) sp. and *Cricotopus*/*Paratrachocladius* remain relatively unchanged throughout the whole sediment record.

#### Nižné Terianske pleso

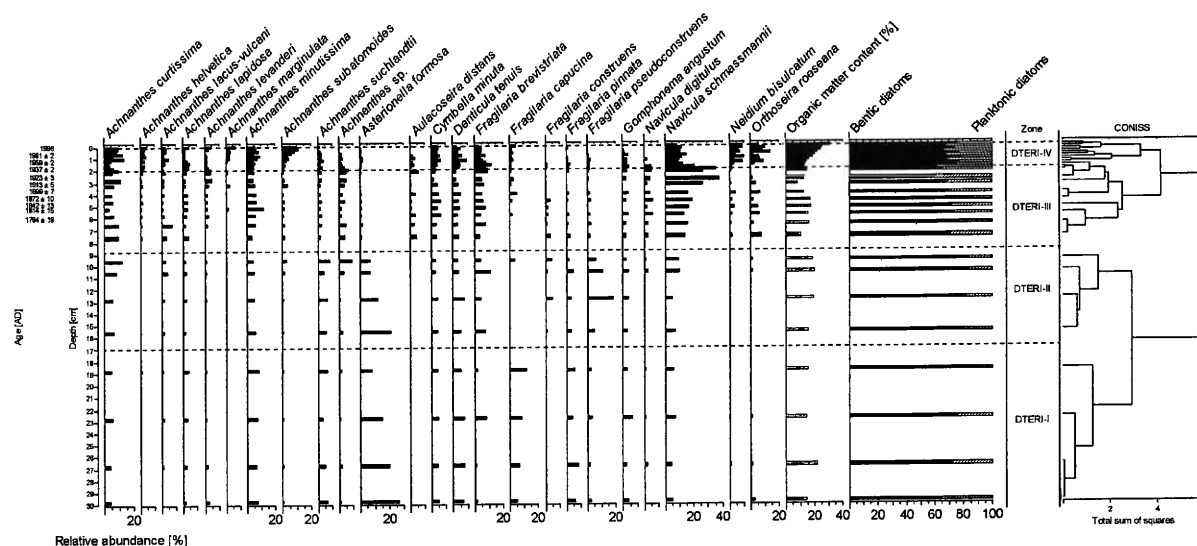
**Diatoms** A total of 110 diatom taxa were identified. Twenty-four species were found at >5% abundance,



**Fig. 2** Changes in percent abundances of selected diatom taxa in the sediment core from Vyšné Temnosmrečinské pleso



**Fig. 3** Changes in percent abundances of chironomid taxa in the sediment core from Vyšné Temnosmrečinské pleso



**Fig. 4** Changes in percent abundances of selected diatom taxa in the sediment core from Nižné Terianske pleso

and ten of them achieved an average abundance of more than 10%.

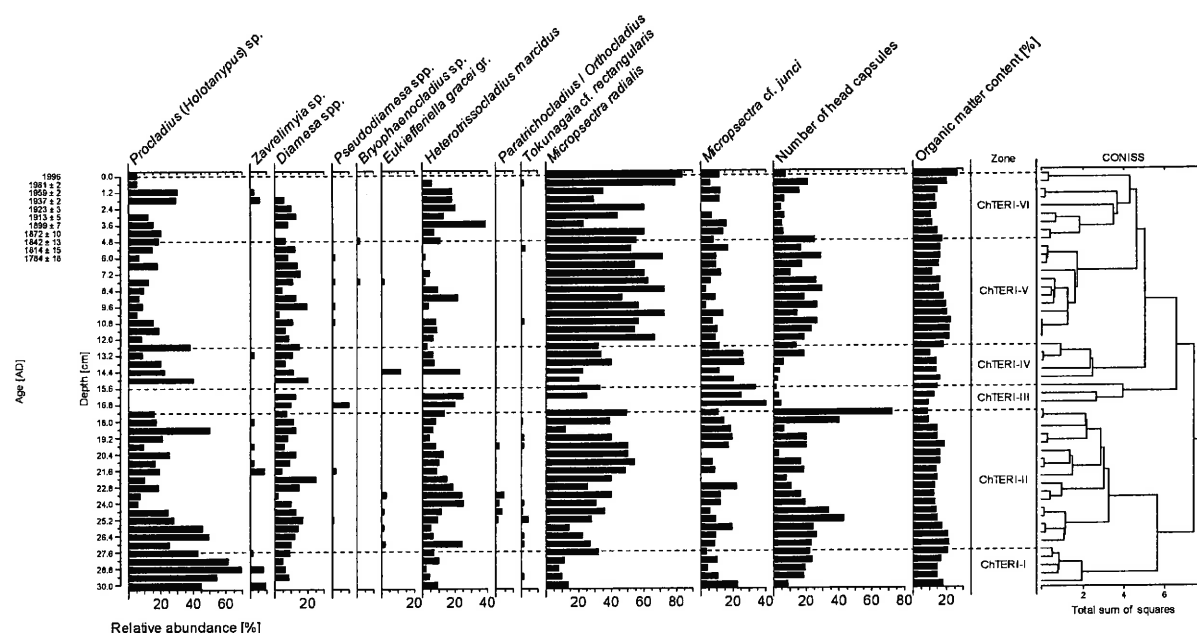
Four diatom zones were identified through the stratigraphically constrained cluster analysis of 28 samples (Fig. 4). Zone DTERI-I (30–17 cm) is clearly dominated by planktonic *Asterionella formosa* (>20%) and together with *Fragilaria pinnata*, *F. capucina*, *Denticula tenuis* and *Achnanthes minutissima* reach their maximum extent in this zone. Zone DTERI-II (17–9 cm) is characterised by a decline in *Asterionella formosa*. *Fragilaria pseudoconstruens* rapidly becomes a major element (19%) and *Fragilaria brevistriata*, *Achnanthes curtissima*, *A. suchlandtii* and *Denticula tenuis* remain relatively abundant in the assemblage. *Navicula schmassmannii* increases throughout this zone and reaches approximately 10% at the top. In Zone DTERI-III (9–2 cm), a major shift in diatoms occurs. *N. schmassmannii* increases gradually and reaches its greatest proportion (up to 40%) at 3–2 cm. On the other hand, *Asterionella formosa* rapidly declines in relative abundance to near extinction. The centric diatom *Orthoseira roeseana*, which was present in very low numbers (1–2%) in the bottom part of the core, significantly increases in number at 8 cm, and becomes a significant member of the assemblage (14%).

Another change in the diatom assemblage is evident in Zone DTERI-IV (2–0 cm). Many species, mostly rare or absent in the deeper zones, appear here

at their highest values. This zone is dominated by *Achnanthes* species (45%), and to a lesser extent by *Orthoseira roeseana* (15%), *Fragilaria brevistriata* (13%) and *Neidium bisulcatum* (9%).

**Chironomids** Altogether 2,211 chironomid head capsules were recovered, comprising 11 taxa. The number of remains was variable, ranging from 1 to 69 specimens per 10 cm<sup>3</sup> of sediment. The most abundant taxa comprising the subfossil record were *Micropsectra radialis* (44.8%), *Procladius (Holotanypus)* sp. (22.4%) and *Micropsectra* cf. *junci* (10.9%). Other important taxa, such as *Heterotrissocladius marcidus* and *Diamesa* spp., were found almost in all of the samples at >9%.

The chironomid diagram is divided into six assemblage zones (Fig. 5). Zone ChTERI-I (30.4–27.6 cm) is dominated by *Procladius (Holotanypus)* sp., making up 40% of the chironomid assemblages. Within Zone ChTERI-II (27.6–17.4 cm), *Procladius (Holotanypus)* sp. declines rapidly, and *Micropsectra radialis*, *Micropsectra* cf. *junci* increase, making up 40% of the chironomid assemblage, along with *Diamesa* spp. and *Heterotrissocladius marcidus*. The numbers of specimens per 10 cm<sup>-3</sup> of sediment vary, with a peak at 18–17.4 cm. The two zones ChTERI-III and ChTERI-IV (17.4–12.6 cm) cover relatively short periods with a rapid, marked decline in the number of chironomid head capsules and consequently in relative abundances of chironomids.



**Fig. 5** Changes in percent abundances of chironomid taxa in the sediment core from Nižné Terianske pleso

*Procladius (Holotanypus) sp.* disappears from the record between 17.4 and 15.6 cm and appears again within Zone ChTERI-IV (15.6–12.6 cm), when *M. radialis* again attains significant relative abundance. In Zone ChTERI-V (12.6–4.8 cm), *M. radialis* continues to be a dominant species with a coincident decrease of *Procladius (Holotanypus) sp.* The decline of relative abundance of *Micropsectra radialis* in Zone ChTERI-VI (4.8–0 cm) is accompanied by a slight increase in *Procladius (Holotanypus) sp.* and a marked increase in *H. marcidus*. *Diamesa* head capsules are missing from the most recent samples. The number of head capsules and organic content in the sediments increase towards the top of the record.

#### Vyšné Wahlenbergovo pleso

**Diatoms** Altogether 112 diatom taxa were identified. The assemblage consisted of planktonic and benthic species, and was dominated by *Achnanthes* species. Twenty-three species occurred at abundances of greater than 5%, eleven of these were found at >10%, four species at >20% and one species at >30%.

Changes in the diatom assemblage can be divided into four zones (Fig. 6). Zone DFU-I (20–15 cm) is characterised by a dominance of *Navicula*

*schmassmannii* (up to 24%) and *Cymbella minuta* (about 15%). *Achnanthes minutissima*, *A. oblongella* (both about 10%), *Fragilaria exigua*, *F. pinnata* and *F. pseudoconstruens* persist as very stable elements of the assemblage in this interval. *Aulacoseira distans* declines in relative abundance from 12% in the bottom layers to 1% in 15 cm. In Zone DFU-II (15–10 cm), *Cymbella minuta* and *Navicula schmassmannii* remain as dominant species (about 20%). A significant increase in *Achnanthes* species (*A. lacus-vulcani*, *A. minutissima*, *A. oblongella*, and *A. subatomoides*) occurs through this zone, reaching up to 30% in some samples. *Aulacoseira distans* making up 10% of the assemblage at the beginning of the zone decreases from 11.5 cm to the top. Zone DFU-III (10–3 cm) shows a gradual reduction in *Navicula schmassmannii* reaching 6% at the top of this interval. In conjunction with this trend, *Achnanthes* species—*A. subatomoides*, *A. lacus-vulcani*, *A. levanderi* and *A. minutissima* become major components of the assemblage (on average 50%). *Cymbella minuta* retains its previous abundance. In the sediments of Zone DFU-IV (3–0 cm), *Achnanthes* species attain significant proportions (50–70%) of the diatom assemblage composition. *Aulacoseira distans* reaches its maximum extent (24%) at 3 cm. *Cymbella minuta* declines in relative abundance similarly to

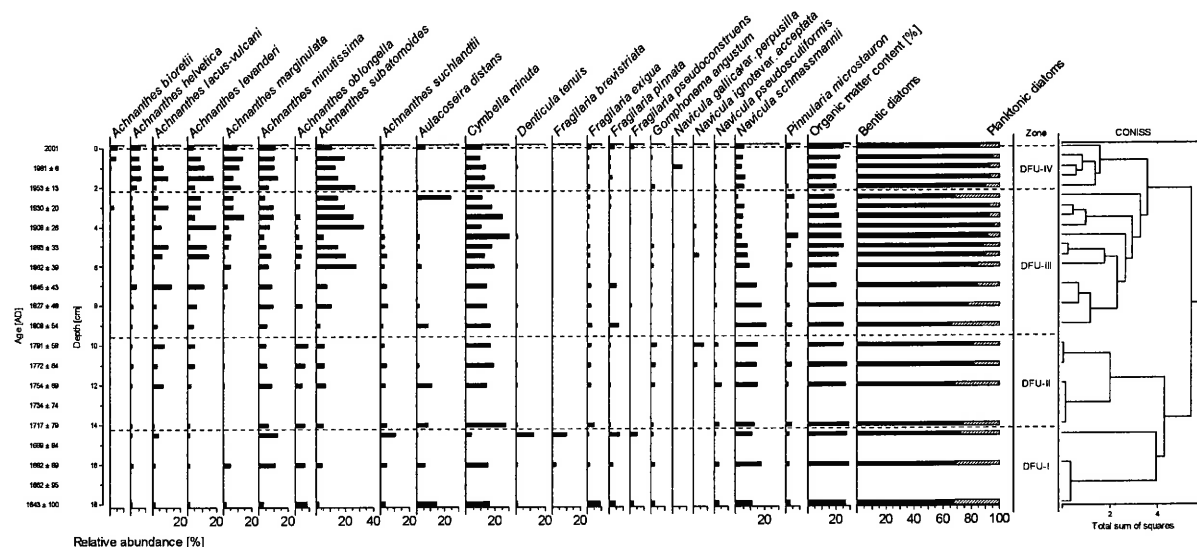


Fig. 6 Changes in percent abundances of selected diatom taxa in the sediment core from Vyšné Wahlenbergovo pleso

*Pinnularia microstauron*, whereas *Navicula gallica* var. *perpusilla* increases up to 7%. *N. schmassmannii* persists as a relatively small proportion of the assemblage.

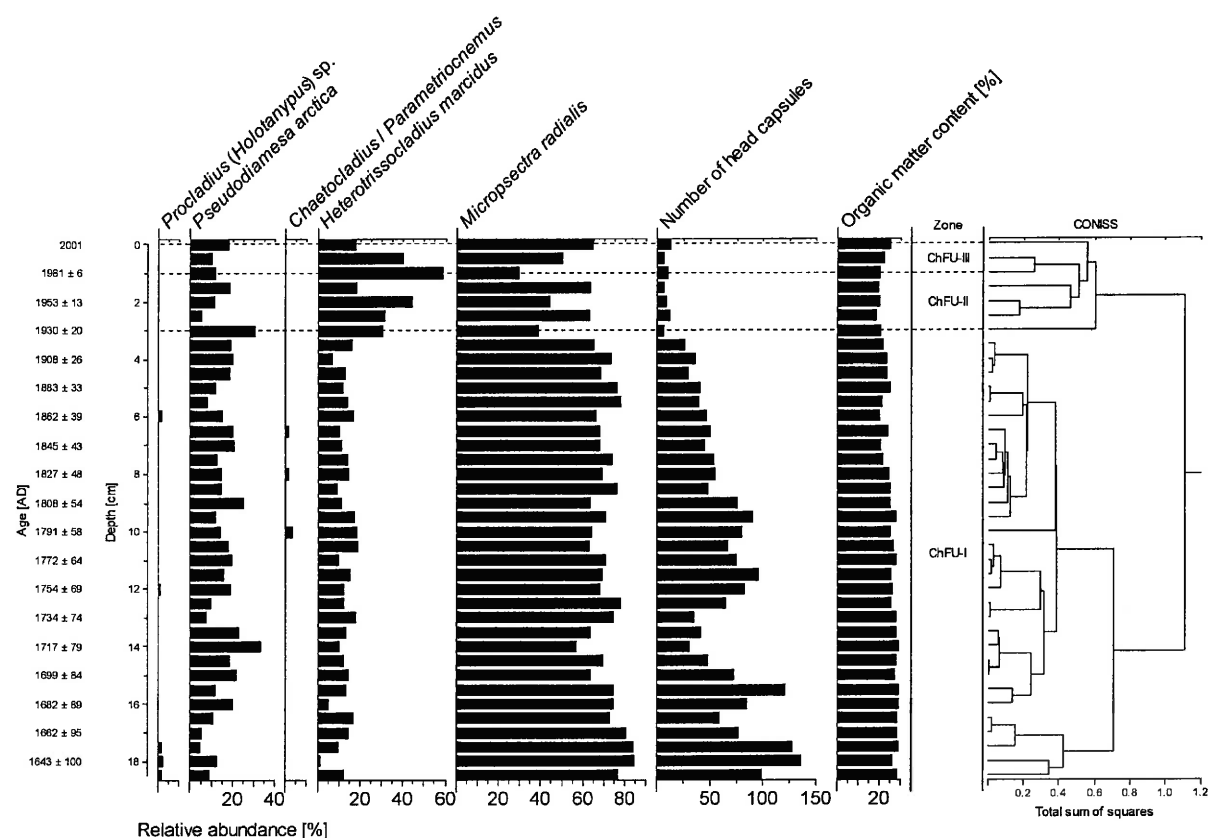
**Chironomids** In total, the chironomid analysis provided 2,048 head capsules from five taxa. The down-core number of chironomid head capsules showed large fluctuations, ranging from 6 to 136 head capsules  $g^{-1}$  dry sediment. *Micropsectra radialis* (68.6%), *Heterotrissocladius marcidus* (14.6%) and *Pseudodiamesa arctica* (16.5%) dominate the whole subfossil record.

Three biostratigraphic zones were identified by cluster analysis (Fig. 7). Zone ChFU-I (19–3 cm) is dominated by *Micropsectra radialis* (>55%). The number of chironomid remains slightly decreased throughout this zone, but declines suddenly from 15 cm to the lowest level at 14–13 cm. In Zone ChFU-II (3–1 cm), *Heterotrissocladius marcidus* rapidly become an important faunal component, whereas *Micropsectra radialis* and *Pseudodiamesa arctica* decline in relative abundances. The upper boundary is marked by a sharp decrease in the number of head capsules. Within the most recent Zone ChFU-III (1–0 cm), *Micropsectra radialis* increases to its previous level, and the abundance of *Heterotrissocladius marcidus* is reduced. The number of chironomid head capsules remains low.

#### Organic matter and subfossil assemblages

The relationship between the abundance of organic matter in the sediments and composition of the subfossil assemblages depends on matrix type (Table 5). A significant predictive power of organic matter is found for all of the abundance matrices. The best prediction is recorded for chironomid assemblages in Vyšné Wahlenbergovo pleso where the proportions of *Pseudodiamesa arctica* and *Micropsectra radialis* increase with the amount of organic matter in the sediments. In general, the strength of this organic matter–assemblage relationship changes inconsistently across groups and lakes: relatively poor results in Nižné Terianske pleso for both of these groups, a higher predictive power for diatoms in Vyšné Temnosmrečinské pleso and a high predictive value for chironomids in Vyšné Wahlenbergovo pleso. The pattern common to all lakes is the increasing proportion of the diatom *Achnanthes levanderi* in the organic-poor layers.

In contrast to the abundance matrices, the amount of organic matter does not appear to be a good predictor of species occurrence in all but one assemblage. A weak relationship is shown in Vyšné Wahlenbergovo pleso, where *Denticula tenuis*, *Achnanthes oblongella*, *Pinnularia subrostrata* and a few other diatom species almost completely disappear from the sediment with lower organic matter content.



**Fig. 7** Changes in percent abundances of chironomid taxa in the sediment core from Vyšné Wahlenbergovo pleso

**Table 5** Percentage cross-validatory fit of predictive CCA models relating diatom and chironomid assemblages to the organic matter content of the three studied lakes

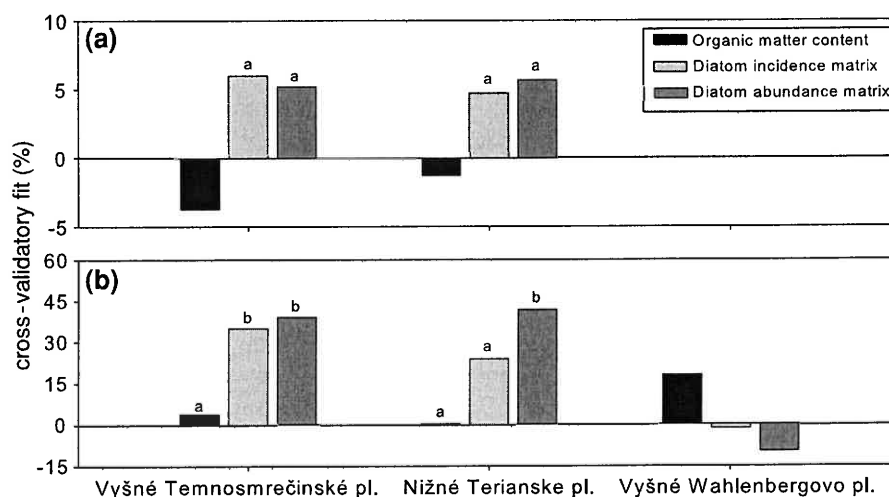
Lake	Incidence matrix		Abundance matrix	
	Diatoms	Chironomids	Diatoms	Chironomids
Vyšné Temnosmrečinské pleso	−0.5	−3.7	6.9	3.7
Nižné Terianske pleso	−1.3	−1.2	0.4	0.7
Vyšné Wahlenbergovo pleso	3.5	–	3.5	17.8

In other cases, organic matter gives negative percentages, and thus has no predictive value for the presence/absence of diatoms and chironomids, respectively.

#### Relationships between assemblages

In two of the three studied lakes, predictive CoCA shows that chironomid assemblages are more closely related to the species composition of diatom

assemblages than to the amount of organic matter in the sediments (Fig. 8). The diatom species expressed either as abundance or as presence/absence, predict the chironomid data better than organic matter content. A notable exception is Vyšné Wahlenbergovo pleso where no relationship between subfossil assemblages is seen. The overall prediction level is higher for quantitative (abundance) than qualitative (presence/absence) chironomid data as judged by cross-validatory fit. The effect of different



**Fig. 8** Chironomid assemblage prediction using different predictors. Prediction levels are given as percentages of cross-validated fit for chironomid composition defined in terms of incidence (a) and abundance (b). Within each

combination of lake and chironomid matrix type, different letters indicate significant differences ( $P < 0.05$ , simple randomisation test). Only predictors with positive fit were included in the pair-wise comparison

diatom matrix types is relatively unimportant. However, the matrix of diatom abundances in Nižné Terianske pleso offers a significantly higher level of prediction than its presence/absence counterpart.

## Discussion

### Biostratigraphies

#### *Vyšné Temnosmrečinské pleso*

Both diatom and chironomid analyses revealed relatively stable taxonomic composition throughout the sediment record. The diatom assemblages are heavily dominated by small *Fragilaria* species reaching more than half of the total diatom abundance. Zone DTE-I ( $\sim$ AD 1044  $\pm$  207 to 1828  $\pm$  37) roughly corresponds to the chironomid zones ChTE-I, II ( $\sim$ AD 1044  $\pm$  207 to 1854  $\pm$  31), though the changes in diatom assemblages are not as marked as they are in the chironomid record. The major change in diatom assemblages started in the middle of the nineteenth century and lasted until recently, whereas the most pronounced change in chironomids took place in the second half of the twentieth century.

It is important to note that compared with other European mountain regions, the Tatra Mountains were

heavily exposed to acidifying pollutants for more than a half of a century, peaking in the late 1980s (Curtis et al., 2005). Though this lake was classified as non-acidified during this acidification period (Fott et al., 1994), the adverse effect of acid conditions on littoral species cannot be excluded. Despite this, we suggest that some factors other than pH-driven changes must be invoked to explain the diatom oscillation through the sequence in this well-buffered lake.

The non-acidified status of this lake during the acidification period (Fott et al., 1994) is supported by the dominance of diatoms *Fragilaria pseudoconstruens* and *Fragilaria pinnata* (Tolotti, 2001). *Fragilaria* species are considered to be highly sensitive to climate-driven variables, too (Schmidt et al., 2004). The ratio of planktonic diatoms to *Fragilaria* species in alpine lakes has been used as an indicator of ice-cover duration, as the number and abundance of *Fragilaria* species may be the result of longer ice-cover period (Lotter et al., 2000). Clarke et al. (2005) hypothesised that changes in the ratio of planktonic to non-planktonic diatoms are associated with the effects of climate warming. They found larger proportion of planktonic diatoms over the last 150 years in many European remote lakes, although indistinct changes were discovered in the Tatra lake district.

Unlike the other two investigated lakes, where the proportion *Fragilaria* species decreased in the upper

parts of the sediment records, the dominance of *Fragilaria* in this lowermost located lake makes the profile difficult to interpret. Other environmental variables might be more important than climate change in explaining the diatom variation.

Fluctuations in relative abundances of *Micropsectra* spp. and the *Tanytarsus lugens* group are crucial for the interpretation of the chironomid sediment record. *Micropsectra* spp. consists of several species including *M. radialis*. Since head capsules were mostly worn, no attempt was made to identify them to the lower taxonomic level. Thus, valuable information on the distribution of *Micropsectra* species throughout the core has been lost.

Only *Tanytarsus bathophilus* from the *T. lugens* group occurs in the modern chironomid fauna of the Tatra Mountain lakes (Bitušík et al., 2006). The species is generally absent in cold alpine lakes and can be found in lakes with higher trophic status (Ekrem, 2004). Considering this, the dominance of *T. lugens* group could indicate a warmer climate during the oldest investigated period (eleventh to thirteenth century).

The decline in the *T. lugens* group and subsequent dominance of *Micropsectra* spp. accompanied by a dramatic decrease in the number of subfossil remains in Zone ChTE-II suggest a cooler climate than was inferred for the previous interval. By extrapolation of  $^{210}\text{Pb}$  dates, we estimated that the shift in chironomid assemblages spans the period between the thirteenth and sixteenth centuries and roughly corresponds with cold periods during the Little Ice Age (Beer et al., 2000). However, since there is a section of the core between 24 and 14 cm in which the bulk density of the sediments is significantly higher than that in the other parts of the core and varies irregularly with depth, dates of sediments below 14 cm (~AD 1700) should be regarded with more caution than those for sediments above this depth. Our interpretation of the chironomid record is consistent with observed chironomid-inferred cooling during the Little Ice Age from the sediments of other European mountain lakes (Lotter et al., 2000, Kamenik et al., 2000, Táτοςová & Stuchlík, 2006).

The increase in the *T. lugens* group between the end of the nineteenth century and recent decades suggests warmer climatic conditions and increased lake productivity. This is in accordance with reconstructed air temperatures for Nižné Terianske pleso

over the last ~200 years (Agustí-Panareda & Thompson, 2002). The appearance of *Paratanytarsus austriacus* during this period is particularly interesting. The subfossil record points to a relatively recent colonisation of the lake. The modern distribution of the species in the Tatra Mountains is restricted to warmer subalpine lakes. Its occurrence in higher situated alpine lakes in the future could be a signal of changes in their temperature regimes.

#### Nižné Terianske pleso

The analyses display a relatively stable taxonomic composition of diatom and chironomid assemblages throughout the investigated period. The important zone boundary in the diatom record is seen at 9 cm, with the most prominent change at 3 cm (~AD 1900). Assemblages dominated by *Asterionella formosa* and *Fragilaria capucina* were replaced by the assemblage with *Achnanthes* spp., *Navicula schmassmannii*, and *Orthoseira roeseana* the dominant species approximately 200 years ago. Šporka et al. (2002) found that the increase in *Achnanthes* species is linked with mean October temperature increases. Further positive relationships between diatoms and summer temperature were found as well. On the other hand, despite the high lake alkalinity, acid deposition cannot be excluded as an important driving force in the change of diatom assemblages. The diatom zones DTERI-I and DTERI-II roughly correspond to chironomid zones ChTERI-I, II, III, IV. The dominance of *Asterionella formosa* could be indicative of cold climate conditions. This planktonic species has low light requirements and is favoured by late-spring overturn after a long period of ice cover (Maberly et al., 1994).

The major changes in the chironomid fauna can be described as a general succession from an assemblage dominated by *Procladius (Holotanypus)* sp. (Zone ChTERI-I) to an assemblage with an increasing importance and dominance of *Micropsectra radialis*. This general pattern is interrupted twice (Zones ChTERI-III, IV, VI). This change from the *Procladius*-dominated assemblage to an assemblage with a dominance of the cold stenothermic *Micropsectra radialis* could possibly be interpreted as a signal of cooler climatic conditions which have extended until recently. The first shift in this cold-adapted assemblage occurs between 17.4 and 13.8 cm. The change

involves the dramatic reduction of *Micropsectra radialis* and the disappearance of *Procladius* (*Holotanypus*) sp., *Diamesa* spp. and *Heterotrissocladius marcidus* from the sediment record. Accompanying this event is the marked decrease in chironomid density and organic matter contents in the sediments. These characteristics indicate that the in-lake production decreased at this time. Moreover, higher density layers at depths of 18 and 16 cm (Appleby, 2000) suggest episodes of rapid accumulation from increased erosion in the catchment. *Micropsectra* cf. *junci* is the only chironomid which increased during this period. As a littoral inhabitant, it may reflect favourable conditions in marginal benthic habitats during prolonged ice cover on the lake. Changes in seasonal oxygen availability during the long winter ice cover and/or during summer stratification could be a possible explanation for the strong decline in profundal taxa. The timing of this shift is unknown, but it evokes the cold climatic event observed in Vyšné Temnosmrečinské pleso.

The second important shift between 3.6 and 1.2 cm (AD 1899  $\pm$  7–1959  $\pm$  2) is characterised by similar characteristics as in the previous. A reduction in *Micropsectra radialis*, *Procladius* (*Holotanypus*) sp. and chironomid remains is accompanied by another episode of rapid sediment accumulation, and a decrease in organic matter content in the sediments. Percentages of *Heterotrissocladius marcidus* and *Micropsectra radialis* are more or less complementary, and a very similar distributional pattern is seen in Vyšné Wahlenbergovo pleso. These observations support Warwick's (1989) opinion on the affinity of *Heterotrissocladius* for sediments with a higher proportion of mineral components. As mentioned in the previous study (Šporka et al., 2002), chironomids as a whole showed no correlation to temperature fluctuations in the last 200 years. Only *Micropsectra radialis* was found to be significantly related to temperature trends. The relative abundance of head capsules mirrored the temperature fluctuations during the studied period, but this trend was interrupted in 1930s and 1940s when amelioration was accompanied with a fall in the abundance. The coincidence of elevated *Micropsectra radialis* abundance with higher temperature may be the result of improved food conditions and suggests the indirect response of this cold-stenothermic species to temperature change. Actually, the negative relationship with

temperature observed in the subfossil record could be the response of the species to restricted food sources. Bitušík & Kubovčík (1999) pointed out the difference between abundant remains of *Diamesa* spp. and other taxa closely associated with stream conditions in the older sediment layers with the absence of them in the recent sediments. The change is considered to be an evidence of a stronger inflow in the past.

#### Vyšné Wahlenbergovo pleso

Unlike chironomids, more pronounced changes in diatom assemblages occurred in this lake. The notable shift in diatoms at 10 cm ( $\sim$ AD 1791  $\pm$  58) is associated with an increase in most *Achnanthes* species and a decline in *Fragilaria* species. Similar to the scheme observed in Nižné Terianske pleso, increase of temperature may be of importance in explaining this trend. Zone DFU-IV (3–0 cm), dominated by small benthic *Achnanthes* species, corresponds to chironomid Zone ChFU-III. Acidophilous species (*Achnanthes marginulata*, *A. subatomoides*, *Aulacoseira distans*, and *Fragilaria exigua*) reflect the acidification period of the lake (Jones et al., 1989; Guilizzoni et al., 1996).

Chironomids show a relatively constant composition throughout the older sediment samples (AD 1624  $\pm$  105 to  $\sim$ 1930s). The assemblage reflects cold, high-alpine conditions (Lotter et al., 2000; Bigler et al., 2006). The rapid decrease of subfossil remains between 17 and 13 cm (AD 1662  $\pm$  95 to 1734  $\pm$  74) in conjunction with a reduction of *Micropsectra radialis* and increased values of *Pseudodiamesa arctica* indicate a cooler period, perhaps corresponded to the coldest phase of the Little Ice Age (AD 1645–1715, Beer et al., 2000). The major shift in the chironomid assemblages is observed at the end of the studied period ( $\sim$ AD 1930s to 2001). This period is characterised by a decrease in *Micropsectra radialis* and an increase in *Heterotrissocladius marcidus*. In conjunction with this trend, the density of subfossil remains rapidly declines and organic matter content decreases relative to the previous zone as a consequence of low in-lake production. This pattern corresponds very well with the period of acidification, when the lake became more oligotrophic (Kopáček et al., 2006). It is interesting to note that none of the chironomid taxa (including acid-sensitive *Micropsectra radialis*) present prior to acidification disappeared during the acidification stage.

This data supports the opinion that chironomids better reflect the lake trophic state rather than acidity (Brodin, 1990) provided that pH does not decrease to near or below 5 (Olander et al., 1997). In the most recent Zone ChFU-I, the decrease in *Heterotrissocladius marcidus* and the increases both in *Micropsectra radialis* and organic matter content indicate a recovery stage after acidification (Kopáček et al., 2006).

#### Response of assemblages to temperature

Subfossil remains in lake sediments may contain valuable information about past climatic conditions. Diatom and chironomid subfossils are widely used in environmental and climate reconstructions (reviewed by Smol et al., 1991; Walker, 1995). However, the reaction of both groups can be different across a range of sites (Battarbee et al., 2002a). We chose both descriptive and correlative approaches to compare the responses of these assemblages. Independent zonations of diatom and chironomid stratigraphies showed corresponding zonation patterns without much asynchrony (see above).

The correlative approach, based on the response of assemblages to organic matter as a temperature proxy, showed inconsistent results across groups and lakes. In general, the species inventory of the lakes was not affected by the temperature variability. However, this is unsurprising as the temperature changes in the Holocene are subtle, and even quantitative-based temperature reconstructions may be rendered insensitive by the overall predominance of common species with wide ecological tolerances (Birks & Birks, 2006). In Vyšné Wahlenbergovo pleso, the disappearance of some diatom species correlated with decrease in organic matter was rather the consequence of acidification stress than climate change (e.g., Tolotti, 2001; Štefková, 2006). The same is true for proportional changes in the chironomid composition in this lake, when dominant taxa responded to low organic matter content due to acidification and subsequently oligotrophication (Kubovčík & Bitušík, 2006).

The relationship between elevated *Achnanthes levanderi* abundance and the lower organic matter content observed in all studied lakes is unclear, and further study is needed to interpret this response.

Irrespective of altitude, the significant predictive power of organic matter reflecting overall temperature governs changes in assemblage compositions.

However, relatively small differences in predictive strengths between groups and its inconsistent change along altitude are difficult to interpret. The organic matter content used here as a simple temperature proxy can be the result of complex influences and rather hard to interpret per se, especially when using single core measurements (Shuman, 2003). Moreover, response of assemblage composition to environmental changes may differ with geographical position of lake and assemblages may be influenced by different environmental factors along altitudinal gradients. Heegaard et al. (2006) showed existence of several critical altitudinal boundaries ('aquatic ecotones') where major changes in assemblages composition occurred. In contrast to those ecotones, rate of compositional change appeared to be relatively low at the centre of altitudinal gradient. This complexity might be the reason for inconsistent results that prevents a straightforward interpretation and comparison of sensitivity of different assemblages to climate variability. We can therefore concur with Birks & Birks (2006) that each proxy takes its own unique place in the ecosystem network and may be used to reconstruct different facets of the ecosystem.

#### Relationships between assemblages

Our results clearly show a strong relationship between diatom and chironomid assemblages in all but one lake (Fig. 7). Biotic interactions between trophic levels (e.g., Jackson & Harvey, 1993; Grenouillet et al., 2008) and similar but independent responses to major environmental gradients (e.g., Allen et al., 1999; Paszkowski & Tonn, 2000) are considered as the most obvious mechanisms behind congruent patterns in assemblages. Direct effects of diatom composition on chironomids are unlikely because grazing on algae is not a dominant feeding strategy for chironomids inhabiting the investigated lakes (Hamerlík, unpublished data). Reasons for the high covariance between assemblages are rather indirect. Diatoms can sensitively reflect different aspects of lake environmental conditions (Stoermer & Smol, 1999). Consequently, diatom assemblage composition integrates and efficiently synthesizes a number of causal factors which may also be relevant for chironomids. Still, possible direct effects cannot be excluded and a combination of both effects can make diatom composition a much better predictor of

the chironomid assemblages than organic matter (cf. Schaffers et al., 2008). Interestingly, diatom abundance matrices contain a certain amount of redundant information for prediction purposes. This means that the most relevant information for chironomids is summarised in the presence/absence of diatoms, or that at least abundance matrices do not offer a higher predictive power than incidence matrices.

In Vyšné Wahlenbergovo pleso, no common trends in the assemblage compositions are observed. One might argue that a unimodal-based technique is inappropriate in the case of relatively stable chironomid assemblage of Vyšné Wahlenbergovo pleso. However, when indirect approach using linear-based technique has been applied (i.e. redundancy analysis of chironomids with the first axis of diatom correspondence analysis in the predictor role), the results remained insignificant. Thus, both the approaches suggest discordant trends in composition of diatom and chironomid assemblages in this lake. This asynchrony probably arises, at least in part, from different response of diatom and chironomid species to acidification of this lake. According to both, the chironomid and the diatom assemblages, the effect of acidification can be tracked back to the first half of the twentieth century. Recently, chironomid assemblage showed shifts that are attributable to recovery, while diatom assemblage remains relatively stable throughout the uppermost layers of core. On the other hand, climatic-driven changes in assemblages of deeper layers (see above) were more pronounced in diatoms than chironomids. Strong decline and even disappearance of some *Fragilaria* species contrasted sharply with relatively slight changes in proportion of chironomid species during the seventeenth and eighteenth centuries. These discrepancies may be a consequence of the fact that chironomid and diatom assemblages may be controlled by different environmental factors (Larocque & Bigler, 2004). Heegaard et al. (2006) showed that different assemblages of aquatic organisms (diatoms, chironomids and cladocerans) differ in rate of compositional change along the same altitudinal gradient, and both the position and strength at the 'aquatic ecotone' differ considerably among the organisms when comparing the rate of change. Thus, the interpretation of the asynchronies between proxies is rather complex. Nevertheless, more robust insights can be gained from studies that quantify a diverse suite of geochemical

and biological time series. Since many organisms exhibit contrasting responses to common environmental forcing, the use of multiple proxies of environmental change can help avoid errors associated with happenstance variation in individual indicators or hidden causal mechanisms (McGowan & Leavitt, 2009). Advances in multivariate numeric techniques such as co-correspondence analysis (or CoCA) (ter Braak & Schaffers, 2004) or co-inertia analysis (Dray et al., 2003) can help rigorously identify common trends in multivariate datasets such as biotic proxies and allow more complex hypothesis testing.

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