

## Aquatic insects of the Bohemian Forest glacial lakes: Diversity, long-term changes, and influence of acidification

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### Abstract

Aquatic insects have been studied in five Czech (Černé, Čertovo, Prášilské, Plešné, and Laka) and three German (Grosser Arbersee, Kleiner Arbersee, and Rachelsee) lakes and their inlets and outlets in the Bohemian Forest. All available historical and present records, as well as many unpublished data were summarised. Of nine insect orders, 70 families, 214 genera, and 373 species/taxa were found in total (Ephemeroptera 20, Odonata 22, Plecoptera 37, Heteroptera 35, Megaloptera and aquatic Neuroptera 3, Trichoptera 46, Coleoptera 58, Chironomidae 113, other Diptera 39). All aquatic insect groups are discussed from the point of view of species richness, influence of acidification, ecological requirements, distributional ranges of species, and species protection. Altogether 215 species/taxa were found in the lakes, where Heteroptera, Coleoptera, and Chironomidae were the most species-rich groups (135 taxa). The lowest number of taxa was recorded in strongly acidified Čertovo Lake and Rachelsee (55 and 56 taxa, respectively); the highest number of species/taxa was recorded in Laka, Plešné and Prášilské lakes (95, 91 and 89 taxa, respectively). Altogether 237 taxa were found in inlets and outlets; Chironomidae, Trichoptera, and Plecoptera prevailed (151 taxa). Based on the cluster analysis of recent species data, the lakes were classified into four groups which primarily reflect characteristics of the lake littoral and water chemistry. Available data on Ephemeroptera, Plecoptera, Trichoptera, and Heteroptera from the past two decades were analysed in order to reveal possible biological recovery from acid stress. A certain degree of recovery has been documented by the increase in species richness of Ephemeroptera and Heteroptera. Yet the lakes have not been colonised by any acid-sensitive species.

*Key words:* lake classification, littoral, stream, atmospheric acidification, biological recovery, biogeography, species protection, Bavarian Forest, Šumava Mountains

## INTRODUCTION

Eight small glacial lakes are located along the historical border between Bohemia and Bavaria in the Bohemian Forest (Šumava in Czech, Böhmerwald in German). Aside from three lakes on the German side (Rachelsee, Grosser Arbersee, and Kleiner Arbersee), five lakes at the Czech side (Černé, Čertovo, Plešné, Prášílské, and Laka) are the only natural lakes in the Czech Republic, thus they belong to most valuable aquatic habitats within the whole country. With an exception of two isolated glacial lakes in the Karkonosze Mountains (Giant Mts.) in Poland, the nearest mountain lake districts are situated in the Alps in Austria and Germany, and in the Tatra Mountains in Slovakia and Poland.

All Bohemian Forest lakes are small, situated at altitudes between 918 and 1087 m a.s.l., and surrounded by Norway spruce forests (Table 1). Their origin and natural history have been reviewed recently by VESELÝ (1994), WEILNER (1997), and VRBA et al. (2000). Approximately since the 16<sup>th</sup> century, pronounced impacts of various human activities, such as local ore prospecting, mining and smelting, glasswork, logging and clear cutting, cattle grazing, water manipulation for timber transport or hydropower production, and fishing and fish introduction in some lakes, have gradually increased (VESELÝ 1994, VRBA et al. 2000, 2003a). Anthropogenic activities certainly have been reflected by more or less pronounced and oscillating long-term environmental changes that likely have been paralleled in changes of biota. However, many of these changes and impacts remained hidden or invisible for centuries, while occasional hydrobiological survey of the Bohemian Forest lakes started 140 years ago (FRIČ 1872, 1874, for review, see VRBA et al. 2000, 2003a). After the World War II, the Bohemian Forest as well as the whole region of central Europe was exposed to heavy atmospheric pollution that peaked in the mid-1980s, followed by a significant drop in both sulphur (S) and nitrogen (N) depositions during the last two decades (KOPÁČEK & VESELÝ 2005). Due to severe acidification, the Bohemian Forest lakes became specific ecosystems, with bacterioplankton and/or phytoplankton largely dominating their pelagic biomass, the complete absence of fish, and significantly reduced or even extinct crustacean zooplankton (VRBA et al. 2000, 2003a,b). While more or less pronounced reversal in lake water chemistry has been documented in all the Bohemian Forest lakes since two decades ago, the first signs of biological recovery in some lakes have been delayed by a decade or more (VRBA et al. 2003a, NEDBALOVÁ et al. 2006). Their biological recovery, however, has been so far documented chiefly by changes in the plankton communities and long-term data on macrozoobenthos have remained largely unpublished yet.

While some groups, such as algae, macrophytes, zooplankton, or fish, have been studied in more detail (see the bibliography about the lakes by VRBA 2000), our knowledge on benthic invertebrates is relatively poor, rather fragmentary, and not fully comparable among the Bohemian Forest lakes; there are almost entirely missing data on benthos of all three German lakes until a recent past (cf. EMEIS-SCHWARZ 1985, SCHÖLL 1989, WEINZIERL 1999, SCHAUMBURG 2000). The first information on aquatic insects were published by FIEBER (1848), DUDA (1884, 1886), KREJČÍ (1890, 1892), FRIČ & VÁVRA (1897), KĽAPÁLEK (1890, 1894, 1903), ŠÁMAL (1920), and some other authors (for review, see ROUBAL 1957). They are mostly valid and provide reliable data on original species diversity of lakes. Yet mainly four Czech lakes (Černé, Čertovo, Prášílské, and Laka) were investigated. An extensive survey in the Rachel Mt. area (THIEM 1906) also covered aquatic insects; however, findings were located only by altitudes, so that those concerning Rachelsee could not be distinguished. A next research of aquatic insect of the lakes took place in the 1950s, when extensive data on Ephemeroptera, Plecoptera, and Trichoptera were collected (KŘELINOVÁ 1962, LANDA 1969, LANDA & SOLDÁN 1989, NOVÁK 1996). In the 1990s, all Czech lakes were explored but those data (P. Chvojka,

M. Papáček, T. Soldán leg.) remained largely unpublished yet; only the most important records on selected species were published (PAPÁČEK & SOLDÁN 1995). After 2000, two surveys of benthic macroinvertebrates of all eight Bohemian Forest lakes were performed. Data of the first survey by M. Jezberová (2002–2003) have never been published, while results of the second survey were summarised in four diploma theses and one paper (SENOO 2009, UNGERMANOVÁ 2009, SVOBODOVÁ 2010, TEXLOVÁ 2010, SVOBODOVÁ et al. 2012). Since a standardised methodology has been used in either survey, the data are comparable and also cover the fauna of lake outlets and inlets. Many additional data, both published (PROCHÁZKOVÁ & BLAŽKA 1999, WEINZIERL 1999, HOLUŠA 1996, 2000, SCHAUMBURG 2000, BITUŠÍK & SVITOK 2006, CHVOJKA et al. 2009, BITUŠÍK 2006, 2011) and unpublished (P. Bitušík, J. Bojková, P. Chvojka, M. Papáček, T. Soldán, J. Sychra leg.), have been accumulated recently. Current distribution of aquatic insects in the sub-littoral zone of three lakes was studied by BARÁKOVÁ (2012). Therefore, the main aims of this study are: (i) to summarise all published and unpublished data on the occurrence of species that have ever been found in the Bohemian Forest lakes, their inlets and outlets; (ii) to evaluate relevance of biogeography and species ecological requirements for the community structure, with a special focus to glacial relict fauna and nature conservation; (iii) to describe long-term trends in distribution of aquatic insects in particular lakes; and (iv) to compare species richness of the Bohemian Forest lakes with other mountain lake districts in Europe.

## STUDY AREA

We studied eight glacial lakes (Fig. 1, Table 1) in the Bohemian Forest (the Hercynian crystalline mountain massive, called Šumava in Czech and Böhmerwald in German; sometimes also referred as the Šumava Mts. or the Bavarian Forest/Bayerischer Wald in regional Eng-

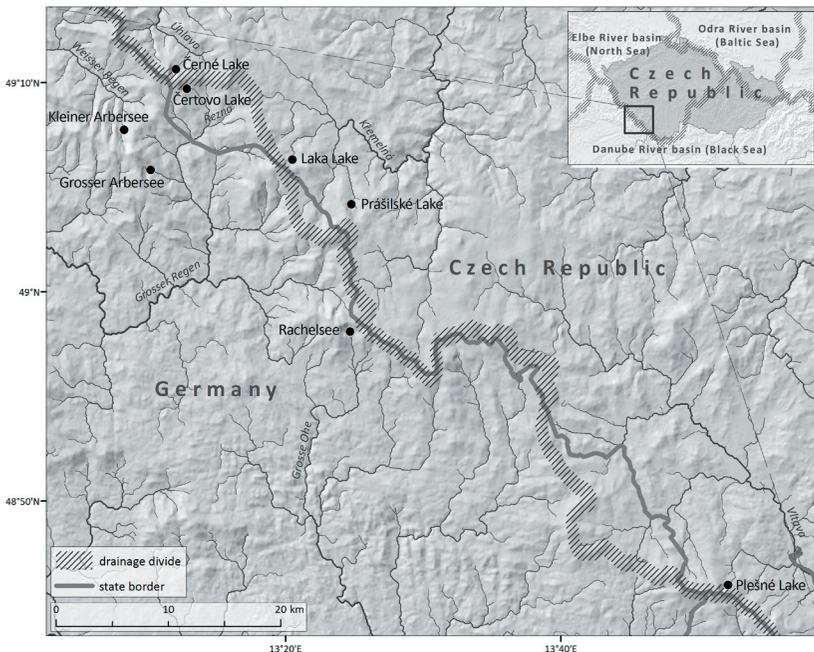


Fig. 1. Map of the studied area showing the location of glacial lakes in the Bohemian Forest.

**Table 1.** Main characteristics of eight glacial lakes in the Bohemian Forest (from VRBA et al. 2000; data on the Czech lakes updated according to JANSKÝ et al. 2005); lakes ordered according to decreasing estimates of theoretical retention times (TRT).

Lake name (used in English)	(C: in Czech) (G: in German)	code	Location		Lake				Catchment			TRT (days)
			latitude	longitude	altitude (m)	surface (ha)	depth (m)	volume (10 <sup>6</sup> m <sup>3</sup> )	area (km <sup>2</sup> )	forest	bedrock	
Černé Lake	C: Černé jezero G: Schwarzer See	CN	49°11' N 13°11' E		1008	18.8	40	2.92	1.24	Norway spruce	mica-schist	661
Čertovo Lake	C: Čertovo jezero G: Teufelsee	CT	49°10' N 13°12' E		1028	10.7	35	1.86	0.89	Norway spruce	mica-schist	587
Plešné Lake	C: Plešné jezero G: Plockensteiner See	PL	48°47' N 13°52' E		1087	7.6	19	0.61	0.67	Norway spruce	granit	277
Prášilské Lake	C: Prášilské jezero G: Stubenbacher See	PR	49°05' N 13°24' E		1079	4.2	17	0.35	0.65	Norway spruce	mica-schist & granit	157
Rachelsee	C: Roklanské jezero G: Rachelsee	RA	48°58' N 13°24' E		1071	5.7	13	0.18	0.58	Norway spruce	gneiss	87
Grosser Arbersee	C: Velké Javorské jezero G: Großer Arbersee	GA	49°06' N 13°07' E		935	7.7	16	0.45	2.58	Norway spruce & beech	gneiss	47
Kleiner Arbersee	C: Malé Javorské jezero G: Kleiner Arbersee	KA	49°08' N 13°09' E		918	9.4	9	0.25	2.79	Norway spruce & beech	gneiss	24
Laka Lake	C: jezero Laka G: Lakka See	LA	49°07' N 13°20' E		1085	2.6	3	0.05	1.02	Norway spruce	gneiss	14

lish literature). As the mountain range forms the principle European watershed between the Danube River basin (Black Sea) and the Elbe River basin (North Sea), four lake catchments belong to either basin. Kleiner Arbersee (drained by the Weisser Regen), Čertovo Lake and Grosser Arbersee (both drained by the Řežná/Grosser Regen), and Rachelsee (drained by the Grosse Ohe) belong to the Danube River basin, whereas Černé Lake (drained by the Úhlava), Laka and Prášílské lakes (both drained by the Křemelná), and Plešné Lake (drained by the Vltava) belongs to the Elbe River basin. The latter, easternmost lake is rather isolated, situated at a considerable distance from other lakes (Fig. 1).

### Water chemistry, trophic and acidification status of the lakes

All studied lakes but one (Laka) are dimictic lakes. Their water chemistry and plankton has been investigated with respect to acidification and recovery of the lake ecosystems during the last decades (e.g., KOPÁČEK et al. 2002, VRBA et al. 2003a). Still a century ago, all the Bohemian Forest lakes were humic brown-water lakes (cf. Table 2 in VRBA et al. 2000); most lakes had more or less neutral pH in the middle of the last century (for review, see VRBA et al. 2000). Available pH values of lake water from the last fifty years shows a marked decrease; all dimictic lakes became chronically acidified (pH around 5 or lower, negative alkalinity) in the mid-1980s, while the shallow Laka Lake used to be acidified only temporarily (Fig. 2). Due to acidification, most of the Bohemian Forest lakes became more transparent (VRBA et al. 2000) and had elevated concentrations (as high as  $>1 \text{ mg.l}^{-1}$ ) of total reactive

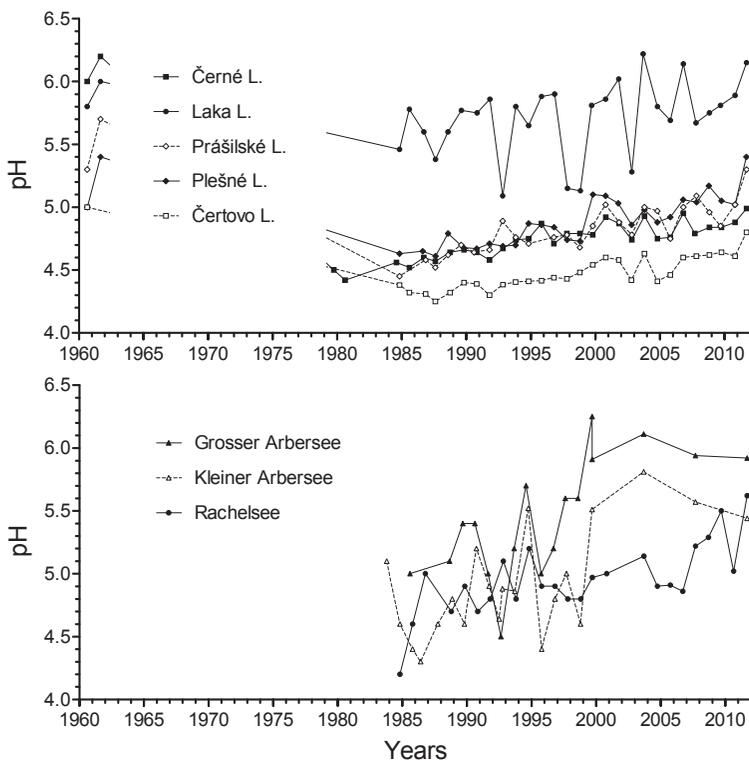


Fig. 2. Long-term data on lake water pH in Czech (top, 1961–2011) and German (bottom, 1984–2011) lakes (according to KOPÁČEK et al. 2002, KOPÁČEK, unpubl. data).

**Table 2.** Selected surface water characteristics of the Bohemian Forest lakes in September 2007 (KOPÁČEK & VRBA, original data).  $Z_s$  – transparency, ANC – acid neutralising capacity, Si – reactive silica, TP – total phosphorus, TON – total organic nitrogen, DOC – dissolved organic carbon, Al<sub>t</sub> – total reactive aluminium, Al<sub>i</sub> – ionic aluminium, Al<sub>p</sub> – particulate aluminium, Chl<sub>a</sub> – chlorophyll *a* (see Table 1 for lake codes).

Parameter / Lake	CN	CT	PL	PR	LA	GA	KA	RA
$Z_s$ (m)	9.1	4.0	0.9	3.7	2.6	3.0	3.5	3.1
pH	4.79	4.59	4.95	4.96	5.29	5.94	5.57	5.22
ANC (mmol.l <sup>-1</sup> )	-17	-31	-11	-10	3	18	10	-5
Si (mg.l <sup>-1</sup> )	1.79	1.52	2.96	1.55	2.07	2.28	1.76	1.89
TP (µg.l <sup>-1</sup> )	2.9	2.6	14.9	5.8	7.2	4.7	5.7	7
NH <sub>4</sub> -N (µg.l <sup>-1</sup> )	53	66	21	22	30	8	15	11
NO <sub>3</sub> -N (µg.l <sup>-1</sup> )	816	437	790	199	690	227	207	346
TON (µg.l <sup>-1</sup> )	186	254	686	331	358	320	282	355
DOC (mg.l <sup>-1</sup> )	1.5	3.5	3.7	5.5	5.9	3.5	4.2	3.2
SO <sub>4</sub> <sup>2-</sup> (mg.l <sup>-1</sup> )	3.14	3.29	2.88	1.70	1.67	2.45	2.68	2.53
Na <sup>+</sup> (mg.l <sup>-1</sup> )	0.74	0.60	0.93	0.64	0.92	0.78	0.79	0.53
K <sup>+</sup> (mg.l <sup>-1</sup> )	0.42	0.24	0.62	0.23	0.52	0.18	0.17	0.32
Ca <sup>2+</sup> (mg.l <sup>-1</sup> )	0.86	0.32	0.93	0.49	0.82	0.84	0.91	0.65
Mg <sup>2+</sup> (mg.l <sup>-1</sup> )	0.41	0.28	0.23	0.31	0.43	0.30	0.32	0.35
Al <sub>t</sub> (µg.l <sup>-1</sup> )	234	309	487	167	188	147	157	264
Al <sub>i</sub> (µg.l <sup>-1</sup> )	182	217	168	44	50	7	17	39
Al <sub>p</sub> (µg.l <sup>-1</sup> )	30	20	215	12	19	48	38	145
Chl <sub>a</sub> (µg.l <sup>-1</sup> )	2.52	3.0	23.5	3.79	2.59	2.53	5.81	6.65

aluminium (Al) with a major proportion of ionic Al, whereas Prášílské Lake had a half Al concentration with the highest proportion of organically-bound Al, which likely allowed for survival of crustacean zooplankton in this lake (VRBA et al. 2003a). Perhaps similar Al contents then occurred in Grosser Arbersee, Kleiner Arbersee, and Laka Lake.

Since the early 1990s, the lake water chemistry has followed – with a characteristic hysteresis – the sharp decline in the regional deposition trends of S and N (KOPÁČEK et al. 2002). Any plankton recovery, however, has been delayed by one to two decades in the lakes (VRBA et al. 2003a). One mesotrophic (Plešné) and three oligotrophic (Černé, Čertovo, and Rachelsee) lakes are still chronically acidified, while four other oligotrophic lakes (Prášílské, Kleiner Arbersee, Grosser Arbersee, and Laka) have recovered their carbonate buffering system (NEDBALOVÁ et al. 2006). The recent lake survey (Table 2) has confirmed a relatively stable chemistry in the epilimnion during the last decade (cf. Table 3 in VRBA et al. 2000 and Table 2 in NEDBALOVÁ et al. 2006), but an increasing trend in dissolved organic carbon (DOC) is obvious in most of the lakes (Table 2 in this study). Sulphate (SO<sub>4</sub><sup>2-</sup>) concentrations have continued in a general decreasing trend in all the lakes, whereas both nitrate (NO<sub>3</sub><sup>-</sup>) and Al concentrations may have fluctuated in response to a changing forest status in the particular catchments (see forest disturbances below). While the largest oligotrophic Černé Lake has more clear water (the highest Secchi depth,  $Z_s$ ), the mesotrophic Plešné Lake is remarkably less transparent compared to all other lakes due to much higher phytoplankton biomass (cf. chlorophyll *a* concentrations in Table 2).

Our research of macroinvertebrates was focused to the littoral zone of the lakes, as well as their inlets and outlets. Thus, our description of the lakes mainly applies to characteristics of their littoral zones restricted to the depth of approximately one meter (Table 3).

**Table 3.** Main characteristics of littoral zone of the Bohemian Forest lakes (see Table 1 for their codes)

Lake	Littoral zone			Littoral vegetation				Inorganic substrate <sup>1)</sup> (%)					Organic substrate <sup>2)</sup> (%)
	<1-m depth (% of total lake area)	sedge, rush (%)	bryophytes (%)	% of total lake perimeter	veget. belt width (m)	prevailing vegetation type	sand	fine gravel	coarse gravel	stones	boulders		
CN	6	0	0	0	0	no vegetation	0	50	15	5	30	60	
CT	5	1	0	1	0.3	no vegetation	50	30	20	0	0	20	
PL	12	9	1	20	8	emergent vegetation	0	80	0	0	20	10	
PR	6	9	1	14	2	emergent vegetation	10	10	30	0	50	10	
RA	14	60	10	52	6	emergent vegetation	30	45	20	5	0	80	
GA	13	20	40	44	1	raised moss carpets	10	70	20	0	0	90	
KA	23	40	40	45	1	raised moss carpets	10	80	10	0	0	90	
LA	8	65	15	36	25	emergent vegetation, raised moss carpets	10	60	20	10	0	90	

<sup>1)</sup> The bottom substrate roughness classified according to HYNES (1970) and GORDON et al. (1992) – simplified: sand (particle size 1.1–2 mm), fine gravel (2–15 mm), coarse gravel (16–64 mm), stones (64–255 mm), cobbles by GORDON et al. 1992), boulders (particle size >256 mm).

## Littoral habitats

The outlets of all eight Bohemian Forest lakes were dammed in the past to control their water level for transporting timber; moreover, bottom sediments used to be removed at least from Kleiner Arbersee and Laka Lake a century ago (for review, see VESELÝ 1994, VRBA et al. 2000). During the last century, however, all the lakes have got a nature reserve status or became parts of the national parks.

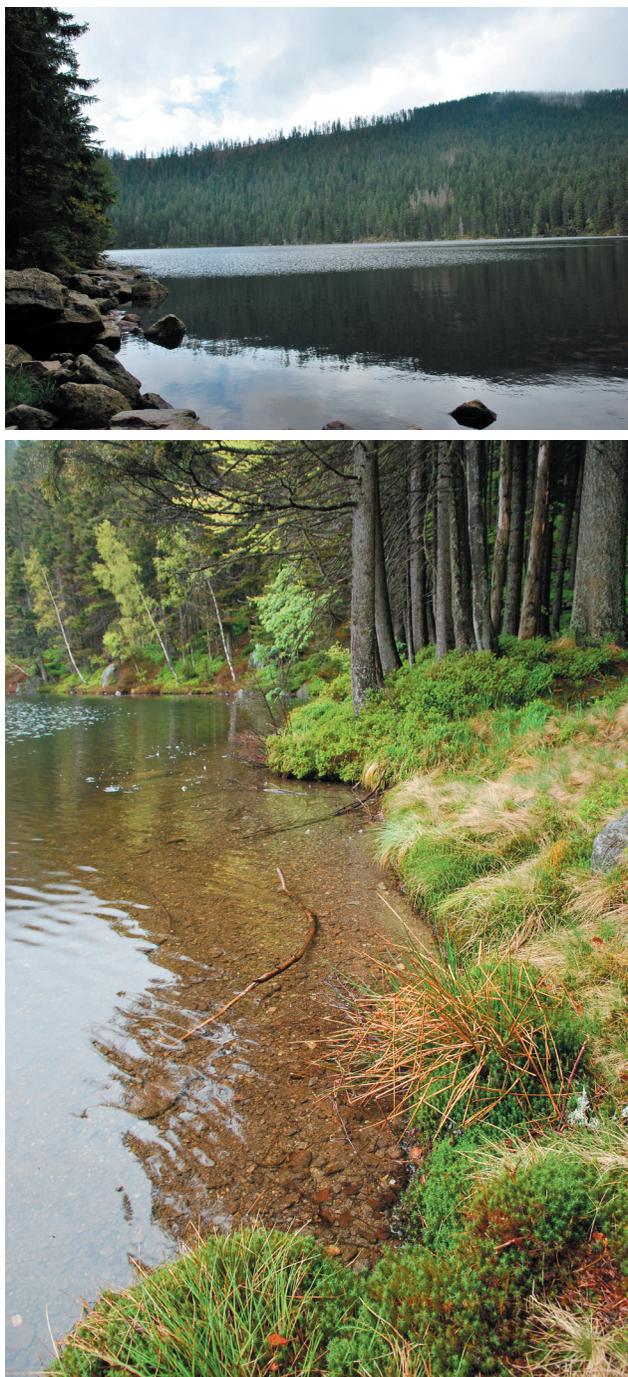
Černé and Čertovo lakes are the largest by both area and volume (Table 1); therefore the share of their littoral is very low (5% and 6%, respectively). Both lakes possess very similar littoral characteristics. Contrary to all other lakes, only negligible part of their littoral is overgrown by aquatic plants, emerged vegetation is nearly missing (Table 3). While mosses are completely missing in Čertovo Lake, only two moss species (*Marsupella emarginata* var. *aquatica* Lindemb. and *Scapania undulata* (L.)) can be sparsely found in Černé Lake. The littoral bottom of Černé Lake consists predominantly of boulders, gravel, and large amount of organic debris (Fig. 3). The littoral of Čertovo Lake consists predominantly of sand and gravel, with considerably lower share of organic debris (Fig. 4, Table 3). A small hydroelectric power plant operates on the outlet of Černé Lake causing certain water table fluctuations within <50 cm depth in the littoral (usually in spring or autumn, when a water reserve is available).

Plešné Lake, Rachelsee, and Prášilské Lake are approximately of the same size, depth, and altitude (Table 1). Their littoral bottom consists predominantly of gravel and sand, and a high share of boulders in Prášilské Lake (Fig. 5–7). All lakes exhibit a belt of littoral vegetation of sedges and rushes with the dominance of *Carex rostrata* Stokes (Table 3). While these belts are situated mostly near inlets' mouths in Prášilské and Plešné lakes, the uninterrupted belt in Rachelsee is surrounding almost the whole lake. In Plešné Lake, the belt of littoral emerged vegetation consists predominantly of bryophytes *Scapania undulata*, *Marsupella emarginata* var. *aquatica*, and *Warnstorfia pseudostraminea* (Müll. Hal.). A relict population of *Isoetes echinospora* Durieu, a submerged aquatic quillwort, forms dense littoral vegetation in a shallow tributary area. In Prášilské Lake, the bryophyte cover is restricted to the only part of lake littoral and consists of dominating *Sphagnum fallax* (H. Klinggr.) and *Sphagnum riparium* Ångström. The littoral zone in Prášilské Lake is considerably smaller (only 6% of the total lake area) than in Plešné Lake and Rachelsee (12 and 14%, respectively).

Grosser Arbersee and Kleiner Arbersee are situated at the lowest altitude, thus they have the largest catchments area (at least twice than that of the other lakes) and very short water retention time (Table 1). They are surrounded by mixed forest with a high share of beech and fir, in contrast to all other lakes that are situated mostly in Norway spruce forests. Great proportions of their water tables are occupied by floating islands of vegetation and/or floating raised moss peninsulas (for details, see WEILNER 1997). Generally, bryophytes dominate littoral vegetation in these two lakes (Fig. 8–9). There are many peat moss species, mostly *Sphagnum fallax*, accompanied by *S. riparium*, *S. flexuosum* Dozy et Molk., *S. cuspidatum* Ehrh., *S. papillosum* Lindb., *S. magellanicum* Brid., and *S. balticum* (Russow), which are predominantly in raised parts of the littoral; therefore, littoral substrate is highly dominated by organic matter (Table 3). Both lakes are frequently visited by tourists; there is even a hotel at either lake. Grosser Arbersee consists of two basins (formed by a glacier, WEILNER 1997) that are artificially separated by floating logs across the lake; an eastern part is commercially exploited (by boating), whereas a western part is strictly protected. Our attention has been paid to the latter part including inlets. The occurrence of yellow water-lily (*Nuphar lutea* (L.)) indicates slightly different conditions of Grosser Arbersee compared to other la-



**Fig. 3.** Černé Lake (May/September 2010, J. Bojková phot.) – a general view from the outlet (top); eastern shore with stony-gravel littoral and organic debris, without vegetation (middle); western shore with the littoral covered by organic debris and occasional occurrence of aquatic mosses (bottom).



**Fig. 4.** Čertovo Lake (May 2010, J. Bojková phot.) – a general view from the outlet (top); north-eastern shore with sandy and gravel littoral, almost without vegetation (occasionally with *Juncus* and mosses, bottom).



**Fig. 5.** Prášilské Lake (May 2010, J. Bojková phot.) – a general view from the main inlet (top); south-western shore with the shallow, sandy-gravel littoral with *Carex rostrata* and occasional *Sphagnum* spp. (middle – habitat of diving beetle *Nebrioporus assimilis*); south-eastern shore with the steep stony littoral, occasionally with *Carex rostrata* (bottom).



**Fig. 6.** Plešné Lake (May 2010, J. Bojková phot.) – a general view from the outlet (top); south-western shore with wide belt of *Carex rostrata* and mosses (middle); north-eastern shore with boulders and the stony-gravel littoral partially overgrown by *Carex rostrata* (bottom).



**Fig. 7.** Rachelsee (May 2010, J. Bojková phot.) – a general view from the outlet (top); north-eastern shore with large belt of *Carex rostrata* (along the shore of almost the entire lake, middle); southern shore near outlet, the only part of the lake with gravel and sandy littoral (bottom).



**Fig. 8.** Grosser Arbersee (September 2010, J. Bojková phot.) – a general view from the outlet, in front, the eastern commercially exploited part, the majority of lake with the coarse, stony-gravel littoral without vegetation (top); western, strictly protected lake part with large belts of *Carex rostrata* and *Sphagnum* spp., and almost completely organic substrate (middle); some areas of the western part are vegetated by yellow water-lily (*Nuphar lutea*, bottom).



**Fig. 9.** Kleiner Arbersee (May/September 2010, J. Bojková phot.) – a general view from the outlet (top); south (middle) and north-western (bottom) shores of the lake. Almost the whole littoral shows a torfaceous character, there are large peat moss (floating) islands and belts; the rest of littoral is overgrown by *Catex rostrata*; bottom substrate is completely organic. Note mixed forests in the background.

kes. Littoral vegetation profiles were mapped in all three German lakes by Š. Husák (WEILNER 1997).

Laka Lake is the smallest Bohemian Forest lake and differs from the others in many respects. It is a shallow polymictic lake, situated in a relatively large Norway spruce catchment at high altitude (Fig. 10). Its theoretical retention time is only two weeks (Table 1). Similarly to both Grosser Arbersee and Kleiner Arbersee, its littoral is dominated by organic matter, because the littoral zone is composed of sedges (*Carex rostrata* in particular), rushes, and bryophytes (Table 3). Floating islands made of peat mosses are moving actively each year, sometimes even dividing the lake into several parts. Submerged bryophytes are dominated by *Sphagnum cuspidatum* and *S. riparium*, accompanied by *S. auriculatum* Schimp. and *Warnstorfia fluitans* (Hedw.).

Lake inlets and outlets represent hypocrenal and epirhithral habitats (Fig. 11).

### Recent forest changes in catchments and surroundings of the lakes

The Bohemian Forest is dominated by subalpine Norway spruce forests at high altitudes (>1050 m a.s.l.), either old-growth or managed ones. Due to historical reasons, planted Norway spruce monocultures replaced original mixed forests of lower altitudes and many spruce forests on the Czech side have been of similar age (over 120 years). Therefore, recent Norway spruce forests in the region have become extremely sensitive to wind gales and bark beetle outbreaks.

A severe windbreak hit spruce forests along the main tributary of Prášílské Lake in 1984. After that, a part of the lake catchment was clear cut with consequent reforestation of Norway spruce. This episode of missing forest vegetation indeed temporarily prevented (in this lake) a regional decrease in  $\text{NO}_3^-$  concentrations (VESELÝ et al. 1998a). As Prášílské Lake became a core zone of the Šumava National Park in 1991, later disturbances in the lake catchment and its surroundings led to further natural forest breakdown and remarkable changes (opening) of the landscape. A bark beetle outbreak in the Bavarian Forest National Park caused a similar subalpine spruce forest die-off in the entire Rachelsee catchment in the late 1990s. Since 2004, the pest has caused Norway spruce die-off around Plešné Lake, where European beech and white fir, as well as natural recovery of Norway spruce are abundant. Another winter gale, the hurricane Kyrill in 2007, caused large-scale disturbances and further bark beetle outbreak in non-intervention zones of the Šumava National Park, including the drainage area of Laka Lake, where, more recently, dead spruce forests have been naturally invaded by rowan ash and Norway spruce.

The catchments of four western lakes remain relatively undisturbed so far. While the corries of Černé and Čertovo lakes were rather deforested for a few centuries (VESELÝ 1994), they were reforested by Norway spruce forests during the 19<sup>th</sup> century. On the other hand, the surroundings of both German lakes, Grosser Arbersee and Kleiner Arbersee, are covered, at lower altitudes, with well developed, more natural mixed forests.

## MATERIAL AND METHODS

### Sampling methods

Sampling techniques have been based mostly on standard hydrobiological and entomological methods. Imagines and larvae were collected in all seasons except the ice-cover period. The littoral was sampled to the depth of approximately 1 m in all lakes. Two or three permanent inlets of each lake were investigated. Astatic habitats (periodical pools) in proximity of the lakes were sampled only occasionally.



**Fig. 10.** Laka Lake (June/September 2010, J. Bojková phot.) – a general view from the outlet (top); north-western shore with large belts and (floating) islands of *Sphagnum* spp. and *Carex rostrata*, bottom almost completely covered with organic substrate (middle); north-eastern shore with the littoral densely overgrown with *Carex rostrata* and predominantly organic substrate (bottom).

Larval assemblages were sampled by semiquantitative kicking sampling method (FROST et al. 1971) using a hand net (0.5-mm mesh size). Sampling was time-limited to 3-minute sampling by JEZBEROVÁ (in 2002–2003, unpubl.), SENOO (2009), and UNGERMANOVÁ (2009), or 5-minute sampling by SYCHRA (in 2010, unpubl.).

Special methods have been applied for sampling of Heteroptera and Chironomidae. Heteroptera were sampled by time-limited sampling using kitchen strainer and floating water light traps in 2007–2011 (M. Papáček leg.). Occasionally, some individuals living in open water were collected by vertical hauls of plankton net from a boat (J. Kubečka and J. Vrba



**Fig. 11.** Lake inlets and outlets (May 2010, J. Bojková phot.) – a cascading inlet of Čertovo Lake, with steep slope and predominantly stony substrate (top left); a cascading inlet of Černé Lake, overgrown by moss carpet (top right); a wide mouth of one tributary to Laka Lake, with gravel substrate, enabling lotic species to colonise the lake littoral (middle left); a branched mouth of the main tributary to Prášilské Lake with a great deal of organic debris (middle right); a man-made part of the outlet of Laka Lake, rich in organic debris, with partly sandy bottom (bottom left); rough-stony and high-slope bottom (rich on mosses) of the outlet of Kleiner Arbersee (bottom right).

leg.). Chironomidae (pupal exuviae, pupae, and imagines associated with exuviae) were collected along the shores of lakes and streams by skimming the water surface with a 200- $\mu$ m mesh hand net attached to an extension pole (BITUŠÍK & SVITOK 2006, BITUŠÍK 2011; J. Kopáček leg.). In the streams, the floating material was collected in accumulation areas and behind obstacles along a distance of approximately 100 m from the lakes (BITUŠÍK & SVITOK 2006, BITUŠÍK 2011; J. Kopáček leg.). PROCHÁZKOVÁ & BLAŽKA (1999) sampled larvae in Černé Lake using Friedinger benthic sampler in 1961.

Other material was sampled qualitatively by a metal strainer of 30 cm in diameter and 0.5-mm mesh size (especially Ephemeroptera, Plecoptera, and Trichoptera) and a standard kitchen strainer with 1.0-mm mesh size (Heteroptera and Coleoptera). This sampling was not time limited and lasted as long as new taxa appeared.

Imagines of Ephemeroptera, Plecoptera, and Trichoptera were collected by sweeping of vegetation along lake shores and inlets/outlets. Imagines of Odonata were collected individually by a hand net. SCHÖLL (1989) collected imagines of Chironomidae by sweeping with a net and by light traps and reared larvae in the laboratory to obtain imagines for the more accurate identification.

More details on the sampling methods are available in the literature cited in species tables.

### Material and its deposition

The vast majority of historical data (1884–1949) was not possible to verify or re-determine since historical material had not been preserved or we have had no possibility to trace it at present. The only exceptions were Trichoptera collected by F. Klapálek in the turn of the 19<sup>th</sup> and 20<sup>th</sup> century and Ephemeroptera and Plecoptera collected by V. Landa and E. Křelínová in the 1950s and 1960s. Recently published as well as unpublished material was mostly determined or revised by authors. The name of determinator is emphasised only provided that it is not identical with the author(s). Details on data used are summarised below.

Unpublished material is deposited in several collections denoted by the following acromyms: DBZ-MUNI = Department of Botany and Zoology, Masaryk University, Brno, Czech Republic; ENT-BC = Institute of Entomology, Biology Centre ASCR, České Budějovice, Czech Republic; ENT-NM = Department of Entomology, National Museum, Prague, Czech Republic; FE-USB = Faculty of Education, University of South Bohemia, České Budějovice, Czech Republic; FS-MBU = Faculty of Science, Matthias Belius University, Banská Bystrica, Slovakia; IES-CUNI = Institute for Environmental Studies, Charles University, Prague, Czech Republic; IHB-BC = Institute of Hydrobiology, Biology Centre, ASCR, České Budějovice, Czech Republic.

**Ephemeroptera** – imagines: CHVOJKA (in 2007, unpubl.; det. T. Soldán); imagines and larvae: LANDA & SOLDÁN (1989), SOLDÁN et al. (1998, 1999; det. T. Soldán); larvae: FRIČ & VÁVRA (1897; not revised), SCHÖLL (1989; not revised), JEZBEROVÁ (in 2002, unpubl.; not revised), SOLDÁN (in 1985, 1986, 1989, 1990, 1999, 2002, 2006, 2009, 2010, all unpubl.; Baetidae det. P. Sroka, Heptageniidae det. R.J. Godunko), UNGERMANOVÁ (2009; rev. T. Soldán), SENOO (2009; not revised), SVOBODOVÁ (2010; rev. T. Soldán). Unpublished material is deposited in ENT-BC (Soldán and Chvojka leg.) and IES-CUNI (Jezberová leg.).

**Odonata** – imagines: KREJČÍ (1892; not revised), PERUTÍK (1957; not revised), SOLDÁN (in 1987, unpubl.; det. J. Zelený), CHVOJKA (in 1991, 2007, unpubl.; det. J. Hájek); imagines and exuvia: HOLUŠA (1996, 2000; not revised); larvae: FRIČ & VÁVRA (1897; not revised), JEZBEROVÁ (in 2002, unpubl.; det. J. Zelený), SYCHRA et al. (2008; rev. M. Straka), UNGERMANOVÁ (2009; not revised), SENOO (2009; not revised), SOLDÁN (in 2010, unpubl.; det. J. Zelený). Unpublished material is deposited in DBZ-MUNI (Sychra and Soldán leg.), ENT-NM (Chvojka leg.), and IES-CUNI (Jezberová leg.).

**Plecoptera** – imagines: KLAPÁLEK (1903; not revised), CHVOJKA (in 1991, 2007, unpubl.; det. J. Bojková), BOJKOVÁ (in 2008, 2009, 2010, unpubl.); larvae: FRIČ & VÁVRA (1897; not revised), SCHAUMBURG (2000; not revised), JEZBEROVÁ (in 2002, unpubl.; not revised), SOLDÁN (in 1985, 1986, 1989, 1990, 1995, all unpubl.; not revised; 2002, unpubl.; det. J. Bojková), UNGERMANOVÁ (2009; rev. J. Bojková), SVOBODOVÁ (2010; rev. J. Bojková); imagines and larvae: KŘELINOVÁ (1962; rev. J. Bojková, except four species collected in Prášílské

Lake, whose material were not preserved: *Nemoura marginata*, *Protonemura hrabei*, *P. montana*, *Leuctra autumnalis*). Historical material of Plecoptera (Klapálek's collection, Křelínová's collection) is deposited in ENT-NM; recent unpublished material is deposited in Bojková's collection in DBZ-MUNI, and in IES-CUNI (Jezberová leg.).

**Heteroptera** – imagines: FIEBER (1848; not revised), DUDA (1884, 1886; not revised), FRIČ & VÁVRA (1897; not revised), ROUBAL (1957; reviewed all older data), SCHÖLL (1989; not revised), PAPÁČEK & SOLDÁN (1995), PAPÁČEK (in 1992, 1996, 1998–2002, 2007–2011, all unpubl.), KMENT & PAPÁČEK (1999, partly unpubl.; det. P. Kment), JEZBEROVÁ (in 2002, unpubl.; det. M. Papáček), KMENT & SMÉKAL (2002; det. P. Kment), SYCHRA et al. (2008; det. J. Sychra), SYCHRA (in 2010, unpubl.), UNGERMANOVÁ (2009; rev. M. Papáček), SENOO (2009; rev. M. Papáček), TEXLOVÁ (2010; rev. M. Papáček). Nymphs: PAPÁČEK (in 2007–2011, unpubl.). Unpublished material is deposited in FE-USB (Papáček leg.), DBZ-MUNI (Sychra leg.), and IES-CUNI (Jezberová leg.).

**Megaloptera** – imagines: Klapálek (1903; not revised), Chvojka (in 1991, unpubl.; rev. J. Špaček); larvae: FRIČ & VÁVRA (1897; not revised), SCHÖLL (1989; not revised), JEZBEROVÁ (in 2002, unpubl.; rev. T. Soldán), UNGERMANOVÁ (2009; not revised), SENOO (2009; not revised), SOLDÁN (in 2010, unpubl.; det. T. Soldán). Unpublished material is deposited in ENT-BC.

**Trichoptera** – imagines: Klapálek (1890, 1894, 1903; rev. P. Chvojka; coll. Klapálek unpubl., rev. P. Chvojka), ŠAMAL (1920; not revised), NOVÁK (1996; leg. V. Landa 1946, leg. K. Novák 1956; not revised), Chvojka (in 1991, 1994, 1999, 2007, all unpubl.), WEINZIERSL (1999; not revised), Chvojka et al. (2009; rev. P. Chvojka), BOJKOVÁ (in 2010, unpubl.; det. P. Chvojka); larvae: FRIČ & VÁVRA (1897; not revised), SCHÖLL (1989; not revised), Chvojka (in 1991, 1994, unpubl.), SCHAUMBURG (2000; not revised), JEZBEROVÁ (in 2002, 2003 unpubl.; rev. P. Chvojka), SYCHRA et al. (2008; det. P. Komzák), UNGERMANOVÁ (2009; rev. P. Chvojka), SENOO (2009; rev. P. Chvojka), SVOBODOVÁ (2010; rev. P. Chvojka). Unpublished material is deposited in ENT-NM (Chvojka and Bojková leg.) and IES-CUNI (Jezberová leg.).

**Coleoptera** – imagines: FRIČ (1872; not revised), FRIČ & VÁVRA (1897; not revised), DOLEŽAL (in 1974, unpubl., det. J. Hájek), HERVERT (in 1977, unpubl.; det. J. Hájek), JELÍNEK (in 1991, unpubl.; det. J. Hájek), NYKLOVÁ (in 2002, unpubl., det. J. Sychra), GAHAI (in 2004, unpubl.; det. J. Hájek), PAPÁČEK (in 2007, 2009–2011, unpubl.; det. J. Sychra), SYCHRA et al. (2008; det. J. Sychra), SOLDÁN (in 2002, 2008, unpubl.; det. J. Sychra; in 2009, unpubl.; det. M. Straka); imagines and larvae: JEZBEROVÁ (in 2002, unpubl.; det. J. Sychra), PAPÁČEK (in 2007, 2011, unpubl.; det. J. Sychra), UNGERMANOVÁ (2009; rev. J. Hájek and M. Fikáček), SENOO (2009; rev. J. Hájek and M. Fikáček), SVOBODOVÁ (2010; rev. M. Straka), SYCHRA (in 2010, unpubl.). Material of Scirtidae (Sychra leg.) was determined by D.S. Boukal and material of Donaciinae (Sychra leg.) was revised by V. Křivan. Unpublished material is deposited in DBZ-MUNI (Sychra, Papáček, Jezberová and Soldán leg.).

**Diptera – Chironomidae** – imagines: EMEIS-SCHWARZ (1985; not revised); pupal exuviae: EMEIS-SCHWARZ (1985; not revised), BITUŠÍK & SVITOK (2006; det. P. Bitušík), BITUŠÍK (2006, 2011; in 2010, unpubl.); larvae: FRIČ & VÁVRA (1897; not revised), SCHÖLL (1989; not revised), PROCHÁZKOVÁ & BLAŽKA (1999; not revised), MATĚNA (in 1999, unpubl.; not revised), SVOBODOVÁ (2010; det. J. Svobodová and J. Matěna). Unpublished material is deposited in FS-MBU (Bitušík leg.) and HBI-BC (Matěna leg.).

**Other Diptera families** – larvae: JEZBEROVÁ (in 2002, unpubl.; not revised), SENOO (2009; rev. P. Pařil), UNGERMANOVÁ (2009; not revised), SVOBODOVÁ (2010; rev. P. Pařil), SOLDÁN (in 2010, unpubl.; det. V. Křoupalová and I. Gelbič). Unpublished material is deposited in DBZ-MUNI, ENT-BC (Soldán leg.), and IES-CUNI (Jezberová leg.).

## Faunistics and biogeography

Although our research was not focused to entomofaunistics of the Czech Republic, we feel that the data presented as “unpublished” results are definitely not negligible from this point of view. There are at least tens of new records or “new quadrat records” in almost all insect orders studied. We did not emphasise these results since enumerating of all records unbridged would make this contribution extremely voluminous. Perhaps an exception can be found in the Odonata chapter, because mapping of dragonflies is very advanced in the Czech Republic and some lakes represented evidently empty quadrates in respective grid maps.

If used, the code number refers to the map quadrates of the central European grid for

mapping flora and fauna (EHRENDORFER & HAMANN 1965), adapted by NOVÁK (1989) and PRUNER & MIKA (1996). To associate unpublished findings with the quadrates, the codes of Bohemian Forest glacial lakes (used for the German lakes in the same way) are as follows: 6845 – Černé Lake and Čertovo Lake, 6846 – Laka Lake, 7249 – Plešné Lake, 6946 – Prášílské Lake, 7046 – Rachelsee, 6844 – Grosser Arbersee and Kleiner Arbersee.

Evaluating distribution of all species collected in the Bohemian Forest lakes (including inlets and outlets), we largely followed basic biogeographic categories and nomenclature (BUCHAR 1983). The following classification has been used for “general distribution”:

(i) Species with large area (LA) comprise species distributed in two or more biogeographic realms (e.g., Holarctic or Palaearctic species occur in the Oriental, Neotropic, Afrotropic, and/or Australian region). Origin of this type of distribution is not distinguished. The species is classified in this category regardless it was artificially introduced or its distribution resulted from, e.g., long distance passive or active migration.

(ii) Species of the Holarctic distribution (HO) comprise species distributed in both Palaearctic and Nearctic regions. Special subcategory of the Holarctic distribution is circumpolar or circumboreal distributional pattern exhibited by species inhabiting the tundra biome in North America and north Eurasia.

(iii) Species of the Palaearctic distribution (PA) comprise species inhabiting Eurasia, North Africa, Middle East, and a part of Arabian Peninsula. The border of Palaearctis is delimited by southern slopes of the Himalayas; however, the border between Palaearctis and the Oriental (Indomalayan) region in the transitory area in China is weakly defined. The Palaearctic region is basically divided into West- and East-Palaearctic subregions. The latter is beyond our interest. The former (WP) covers Europe, including Iceland, Macaronesia (the Azores, Madeira, and Canary Islands), North Africa (Maghreb, north of the Sahara, including the Hoggar (Ahaggar) Mts. and the Tassili Plateau) and the Mediterranean Islands (including Cyprus), and the Caucasus. To the east and north approximately along the Russian–Kazakhstan border and western slopes of the Ural Mountain range to the Kara Sea and Novaya Zemlya. We suggest using the term “Eurosiberian” distribution with caution, because it can include species distributed in Europe and westernmost Siberia as well as the species distributed throughout the whole Palaearctic region. To describe the latter distributional type, we prefer the category of “transpalaearctic” distribution (ZHILTZOVA 1997), which comprises species with a distribution near to the area from the British Islands eastward to Japan or Russian Far East. Similarly, the often used term “European” distribution is misleading, since Europe is only a part of the Westpalaearctic subregion; in other words, the term is only of a geographic sense but definitely not possessing any biogeographic meaning.

Since the Bohemian Forest lakes are situated very close to a geographic centre of Europe, we cannot avoid detailed classification of species from the point of view of the Westpalaearctic subregion. In this case, we are forced to use rather geographic classification since details on the origin and faunistic centres are not exactly known in most species. The origin of species has been described mainly in Ephemeroptera (JACOB 1972, 1979, 1993, HAYBACH 1998, 2003, 2006) and Odonata (ASKEW 1988, MERRITT et al. 1996, WILDERMUTH et al. 2005, DOLNÝ et al. 2007), but our information on other groups is mostly based on individual area (state) records on the species in question.

To simplify the evaluation of distribution of “European” species, the Westpalaearctic subregion is classified as follows:

(i) The West European area is spread from the Iberian Peninsula and the British Islands, through France, Benelux to western Germany (Bavaria) (the Bohemian Forest lakes lie just in the transitory area). It summarises species of the Atlantic and Atlanto-Mediterranean (West Mediterranean) origin.

(ii) The South-Central European area comprises the Mediterranean area and a part of central Europe. The species are distributed in the both European parts. Its northern limits are situated in the Thuringian Forest, some Sudetes (e.g., the Krkonoše/Karkonosze (Giant) Mts. and the Jeseníky Mts.), and the Carpathians (e.g., the Beskydy Mts., the Tatra Mts., Bieszczady Mts., and the East Carpathians). The limits of areas approximately follow the maximal (southernmost) border of the last (Würm/Wisla) glaciation. Such species are often called “submediterranean”. However, this term is sometimes used to describe species living southwards the above borders but not distributed in the Mediterranean itself, or for any species living in the southern half of Europe. To avoid any confusion, we strictly reserved this term to South-Central European species as defined above.

(iii) The North-Central European area consists of Fennoscandia, Baltics, Kola Peninsula, and north European Russia including Novaya Zemlya and the Polar Ural Mts. Its southern limits approximately follow the northern border of South-Central European area.

(iv) The Central European area consists of some parts of the Alps in Austria, Bavaria, and Switzerland, central European Hercynian mountains, the Western Carpathians, and Hungarian (Pannonian) Plain.

(v) The East European area is spread from the East Carpathians, through the Dnieper River and Volga River basins, to the Ural Mountains. The southern limit is the Caucasus and Crimean Peninsula.

Some areas are certainly overlapping. For instance, South-Central and Central European species can overlap in relation to size of their area or West and Central European due to distribution in the Alps, which are included in both areas. Similarly, the Eastern Carpathians are included in both Central and East European areas. Moreover, some species are difficult to strictly classify within these areas, because of their area extension and disjunction. For example, North-Central European species can exhibit conjunctive area or disjunctive area, the most often type of which is boreo-montane or arcto-alpine disjunction.

As indicated above, our knowledge on distribution of individual species is sometimes very fragmentary. We failed to classify other Diptera than Chironomidae, because there are no reliable or summarising literature sources. Evaluation of distribution of individual insect orders is based on the literature sources as follows: Odonata – ZELNÝ (1972, 1992), ASKEW (1988, 2004), DOLNÝ et al. (2007); Ephemeroptera – JACOB (1972, 1979, 1993), HAYBACH (1998, 2003, 2006), BUFFAGNI et al. 2009, BAUERNFEIND & SOLDÁN (2012); Plecoptera – ZHILTZOVA (1997, 2003), GRAF et al. (2009), TESLENKO & ZHILTZOVA (2009); Heteroptera – JOSIFOV (1986), JANSSON (1986, 1995), SAVAGE (1989), POLHEMUS (1995a,b,c), AUKEMA & RIEGER (1995), KANYUKOVA (2006), GRANDOVA & PROKIN (2012), JEZIORSKI et al. (2012), KLEMENTOVÁ (2012); Trichoptera – GRAF et al. (2008), IVANOV (2011); Megaloptera – HÖLZER et al. (2002), ELLIOT (2009); Coleoptera – HANSEN (1987), HOLMEN (1987), ANGUS (1992), NILSSON & HOLMEN (1995), VAN VONDEL & DETTNER (1997), HEBAUER & KLAUSNITZER (2000), BOUKAL et al. (2007), NILSSON (2011), SHORT & FIKÁČEK (2011); Chironomidae – SÆTHER & SPIES (2007); and THE CHIRONOMID HOME PAGE.

The classification of several insects' groups to European subareas was partially based on literature sources ranging the species to European bioregions according to ILLIES (1978).

### **Protection status of species**

Treating insect species of the Bohemian Forest lakes from the point of view of species conservation, we have adopted largely accepted species status according to the IUCN Red List of Threatened Animals suggested by BAILLIE & GROOMBRIDGE (1996) and BAILLIE et al. (1995, 2004), which in many respects meet requirements for ranking any species within the existing categories (cf. PRIMACK 2002, ŠKORPIK 2005). Nevertheless, a strict application of all

evaluation criteria is impossible due to enormous species diversity of insects, sometimes extremely high abundance and wide ecological range, on the one hand, as well as deficiency of data, on the other hand (see also detailed discussion by PLESNÍK 1995a,b, PLESNÍK & ČEPÁKOVÁ 2005). As the classification of protection status may differ at the national scale, the following simplified categories have been applied.

Evaluated species, i.e. those at which any protection is considered necessary, consist of five groups as follows: regionally extinct (RE) – species not recorded for the past 30 years; critically endangered (CR) – species showing well documented trend to become extinct or solitary, often living at a single locality and showing extremely low population density; endangered (EN) – species showing a long-term decline in its occurrence, or living in the “area pejus” within the Czech Republic, though still abundant in the “area optimum”; vulnerable (VU) – species generally meeting the requirements of the EN category but to an evidently lesser extent; and near threatened (NT) – sparsely distributed species of a narrow ecological range, usually subdominant or recessive.

Contrary to FARKAČ et al. (2005), we decided to employ the data deficient (DD) species category. The DD species constitutes the only “inadequate data” category, contrary to all the above categories representing “adequate data” (the “1996 IUCN Red List”, BAILLIE & GROOMBRIDGE 1996). This category, although supposed transitory, is clearly defined. It facultatively gathers the species with largely unknown biology and fragmentary data on distribution that intuitively could fall in some of the above categories in the future. In our evaluation, this category should comprise also the species newly established and those, the status of which was revised after 2005.

The not evaluated (NE) category summarises all the remaining species, i.e. those not requiring any protection. Though the category seems to be easily defined, in the case of aquatic insects, it is sometimes difficult to decide, which species are really “ubiquitous, opportunistic, or common everywhere in high densities”, since there are nearly no habitats in an actual natural state within the Czech Republic. Hence, like in numerous other insect groups, the question of proportionality between evaluated and not evaluated species remains crucial in aquatic insects in question, as well. According to our opinion, at least 40–70% of species should be treated and this opinion roughly corresponds to other invertebrate taxa so far studied from the point of view of biodiversity protection in the Czech Republic (cf. FARKAČ et al. 2005).

### **Comparison of species (taxa) diversity with other European lake districts**

To discuss species diversity of the Bohemian Forest lakes, we have selected recent synoptic literature dealing with macroinvertebrates of European lakes. We included studies from different geographic regions (British Islands and Fennoscandia, the Pyrenees, the Alps, the Carpathians, and Balkans) and different altitudes: lowland lakes in Denmark and Finland (BRODERSEN et al. 1998, HEINO 2008), highland lakes in Scotland (KERNAN et al. 2009a), and montane lakes at 1500–2800 m a.s.l. in the Pyrenees (DE MENDOSA & CATALAN 2010), the Alps (FÜREDER et al. 2006, BOGGERO & LENCIONI 2006, OERTLI et al. 2008, MARCHETTO et al. 2009), and the Tatra Mts. (KRNO 1991, KOWNACKI et al. 2000, KRNO 2006, KRNO et al. 2006, ČIAMPOROVÁ-ZAŤOVIČOVÁ et al. 2010, ČIAMPOROVÁ-ZAŤOVIČOVÁ 2011). A special attention in our comparison has been paid to the nearest lake districts, the Alps and the Tatra Mts., which have been studied in considerable details. According to KERNAN et al. (2009c), littoral macroinvertebrate assemblages of the Tatra Mts. differ from those in central Europe (the Alps), and are more similar to those in the Balkans (the Retezat Mts. and the Rila Mts.). The distance of the Bohemian Forest lakes to the Tatra lakes and to those in the Tyrolean Alps is nearly identical. The crucial question seems to be whether the Bohemian Forest lakes could be

grouped with the lakes in the Alps, the Carpathians, or those in any other lake district.

To compare the species richness of our lakes with species richness of individual European lake districts, we used only recent data (2002–2011) collected in the lakes' littoral (i.e., 196 species/taxa) not to overestimate the species richness by long-term research of our lakes. We compared the number of species/taxa found in total and in particular insect groups, and the number of identical species/taxa. Due to considerably different taxonomic levels used in the literature data in comparison with our data, which were identified predominantly to the species level, we had to consider some taxa of different level identical: for example, *Sialis* or Sialidae identical with *Sialis lutaria*, *Sisyra* sp. identical with *S. nigra*, Corixidae indet. identical with any genus of Corixidae, etc. Consequently, the number of identical taxa seems to be overestimated, but we can suppose that numerous higher taxa of most of the authors in fact include more than one species (even genus).

## RESULTS AND DISCUSSION

### Species richness of insects groups and habitats

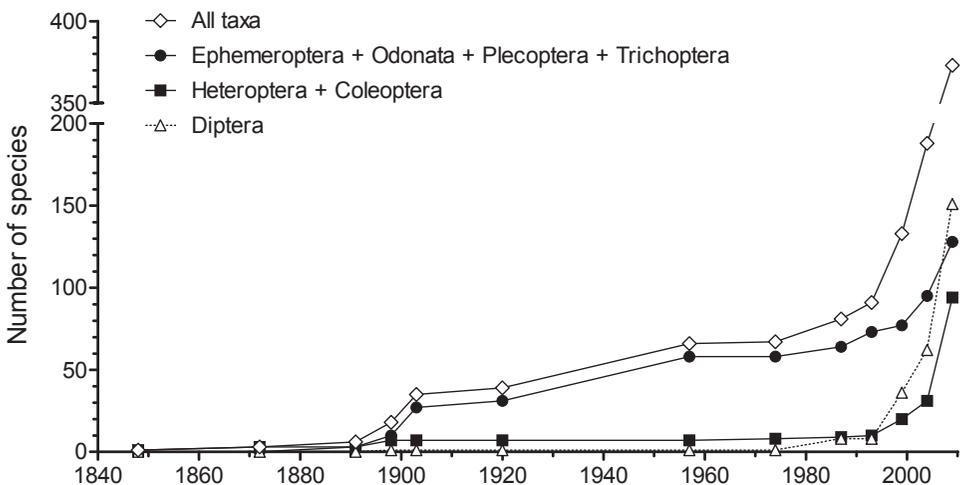
#### History of the research on aquatic insects

Our present knowledge of the diversity of aquatic insects of the Bohemian Forest lakes developed gradually from 1848 (Fig. 12) when the first species, the aquatic bug *Glaenocoris propinqua*, was recorded from Černé Lake (FIEBER 1848). Some 23 years later, two species of aquatic beetles, namely *Gyrinus substriatus* (as *G. natator*) and *Hydroporus palustris*, were collected at the same lake (FRIČ 1872). The third order, Odonata, was reported from the Bohemian Forest lakes within the past decades of the 19<sup>th</sup> century (KREJČÍ 1890, 1892, FRIČ & VÁVRA 1897). The latter reported 14 species of all the insect groups known till the present, of these the orders Ephemeroptera (1 species), Plecoptera (2 species), Megaloptera (1 species) and Diptera (1 species of the family Chironomidae) were recorded for the first time.

Since then, increasing knowledge of species of individual insect orders apparently exhibits two distinctive patterns (Fig. 12), depending on individual authors' scientific interests and specialisation, and collecting endeavour devoted to individual taxa in the course of the last 120 years. The first pattern is shown by the orders Ephemeroptera, Odonata, Plecoptera, and Trichoptera (Fig. 12). Earlier knowledge dates from the 1890s with an initial number of 1–5 species determined (KLAPÁLEK 1890, 1894, FRIČ & VÁVRA 1897) and continues in the first decades of the 20<sup>th</sup> century by new records of several species especially in Trichoptera and Plecoptera (KLAPÁLEK 1903, ŠÁMAL 1920). These authors published new area records on 8 species of Plecoptera and 15 species of Trichoptera to extend the knowledge of the insect diversity of the lakes to 41 species/taxa in this initial period of research. For the following 30 years, a total stagnation of the research of the lake fauna occurred (Fig. 12). As late as in the 1950s, a targeted faunistic research of Ephemeroptera, Plecoptera, and Trichoptera (EPT) led to an increase in the known insect diversity of the lakes to 68 species/taxa. Of these, 26 new records belong to EPT groups, although, except for Plecoptera (KŘELINOVÁ 1962), the results were published much later (LANDA 1969, LANDA & SOLDÁN 1989, NOVÁK 1996). In Odonata, there were no more data from 1897–1960 except for the finding of a dragonfly, *Leucorrhinia dubia* by PERUTÍK (1957) in Černé Lake. Although the research informally continued in 1970–1990 as well, an increase in known species was not pronounced during this period. Strong increase in species knowledge up to final 128 recorded taxa (Fig. 12) is a result of intensive research of the impact of acidification and recovery of lakes carried out from the 1990s to the present.

In contrast to a gradual increase in knowledge of the former group, Heteroptera, Coleoptera and Diptera (including the family Chironomidae) exhibit a quite different pattern (Fig. 12). There were initial records of 1–3 species from the past quarter of the 19<sup>th</sup> century (cf. FRIČ 1872, FRIČ & VAVRA 1897) and then a pronounced stagnation of knowledge occurred for the next nearly 100 years (Fig. 12). The only exception within this period is the first record of a diving beetle *Agabus (Gaurodytes) guttatus guttatus* in Černé Lake (in 1974 by DOLEŽAL, unpubl. result) and several species of Chironomidae (EMEIS-SCHWARZ 1985, SCHÖLL 1989). An amazing increase in knowledge of these groups occurred after 1996. While the number of Heteroptera species increased more than three times (from 10 species known in 1991–1996 to 35 species at present) and the number of Coleoptera species increased from 5 in 1991–1996 to 58 at present, the steepest increase showed the number of Diptera species records (i.e. Chironomidae and “other” Diptera), which increased from 8 species known in 1991–1996 to 151 species at present.

The final period of research of insect species diversity of the Bohemian Forest lakes started in the early 1990s, when the lakes became accessible to scholars, and to the public. Before 1989 indeed, an “iron curtain” almost totally isolated Czech lakes into an inaccessible zone. The present, unusually high species diversity of 373 species/taxa (Table 4) has mainly been achieved thanks to directed research projects and a sampling effort devoting an attention to all habitats and lakes. In 2002–2003, JEZBEROVÁ (unpubl. results) recorded 69 species of aquatic insects. In 2005–2009, SENOO (2009) referred to 93 taxa (71 determined to the species level) in 79 genera and 41 families (including Tricladida, Mollusca, Hirudinida, Nematoda and Oligochaeta) found in the outlets and inlets of the lakes. UNGERMANOVÁ (2009) found 77 taxa (50 determined to the species level) of 39 genera and 26 families (including Mollusca, Hirudinida, and Oligochaeta) in the lake littorals. Most recent additional references are based on a synoptic survey of the lakes in 2008–2011 and an analysis of earlier unpublished data; more than 100 species are presented here as unpublished results.



**Fig. 12.** Species diversity of individual insect groups in the Bohemian Forest lakes within the period of 1842–2011, cumulative increase of knowledge and its historical development (considered only the taxa determined at the species level, other taxa excluded from all groups; family Chironomidae summarised with other Diptera families; Megaloptera and aquatic Neuroptera not shown).

**Table 4.** Total numbers of taxa (both historical and recent findings, 1848–2011) of individual aquatic insect groups found in the Bohemian Forests lakes, their inlets, and outlets.

Order/family/group	Ephemero- ptera	Odonata	Plecoptera	Hetero- ptera	Megaloptera, Neuroptera	Trichoptera	Coleoptera	Chirono- midae	Other Diptera	Total
Families	6	5	7	10	2	12	10	1	17	70
Genera	10	12	12	19	2	32	31	61	34	214
Species/undetermined taxa	20	22	37	35	3	46	58	113	39	373
Species	19	20	32	34	3	44	57	81	12	302
Undetermined taxa	1	2	5	1	0	2	1	32	27	71
Species/taxa in lakes (L)	9	21	15	35	3	19	52	48	13	215
Species/taxa in inlets (I)	4	2	31	1	2	27	16	17	23	123
Species/taxa in outlets (O)	15	10	22	5	2	17	19	75	21	186
Common species/taxa in L+I	2	2	12	1	2	5	13	6	4	47
Common species/taxa in L+O	4	9	8	5	2	3	14	17	3	65
Common species/taxa in I+O	4	2	18	1	2	12	11	8	14	72

**Table 5.** Total numbers of species/taxa found in the Bohemian Forests lakes, their inlets, and outlets (see Table 1 for lake codes) based on both historical and recent findings (1848–2011).

Species/taxa / Lake	CN	CT	PL	PR	LA	GA	KA	RA
Total	111	132	132	143	197	122	110	87
Lakes (L)	76	55	91	89	93	81	73	56
Inlets (I)	48	53	36	47	55	35	30	23
Outlets (O)	25	72	42	54	99	26	28	23
Common in L+I	19	14	14	11	14	6	2	7
Common in L+O	14	23	22	24	22	8	7	4
Common in I+O	17	21	11	17	23	8	12	7

## Species/taxa richness of the lakes and their inlets/outlets

In total 373 species/taxa belonging to nine aquatic insect orders, 70 families, and 214 genera have been recorded in the Bohemian Forest lakes and their inlets/outlets so far (Table 4). The majority of them have been determined to the species level (302 species; 81%). Sixty nine taxa determined at higher than species level comprised especially historical (literature) records, which could not be revised, because the material was not available, and dipterans determined to the genera or species-group levels due to insufficient knowledge of morphology of their larvae.

Besides small groups of Megaloptera and (aquatic) Neuroptera, higher taxa presented within the Bohemian Forest lakes and their outlets/inlets can be divided into three groups according to the absolute number of species/taxa determined (based on VAŇHARA & KUBÍČEK 1999): (i) eudominant Diptera, (ii) dominant Trichoptera and Coleoptera, and (iii) subdominant remaining orders. Eudominant Diptera (altogether 152 species/taxa, 41% of the total) were dominated by the family Chironomidae (113, 30%). The highest species richness of Chironomidae (75 species/taxa) was found in outlets, whereas they were relatively species-poor (17) in inlets. Other Diptera families were collected mainly in inlets and outlets (30) and only 13 taxa were found in the lakes. Dominant Trichoptera (46) and Coleoptera (58) shared a comparable deal (12% and 16%, respectively) of insect fauna of the Bohemian Forest lakes including inlets/outlets. However, far more species/taxa of Coleoptera (52) than Trichoptera (19) have been found in the lakes (Table 4), while the opposite was true for the inlets and outlets. Plecoptera (31) and Trichoptera (27) dominated the insect fauna of the inlets (Table 4).

Altogether 215 species/taxa (58%) were found in the lakes' littoral, where Heteroptera, Coleoptera, and Chironomidae were the most species-rich groups (135 species/taxa). The lowest number of species/taxa was recorded in Čertovo Lake and Rachelsee (55 and 56, respectively; Table 5). Most probably, these lakes lost their original species richness due to strong long-term acidification in the past (Fig. 2). Čertovo Lake and Rachelsee are followed by Kleiner Arbersee and Černé Lake (73 and 76, respectively), and Grosser Arbersee (80). The highest species richness was recorded in Laka, Plešné and Prášílské lakes (93, 91, and 89, respectively). Each of these lakes has a specific character, which could mitigate the effects of acidification and/or offer suitable conditions for invertebrates. Laka and Prášílské lakes have got the highest recent DOC concentrations (Table 2) and historically low Al concentrations (cf. VRBA et al. 2003a). Laka Lake is an exception within Bohemian Forest lakes due to very short retention time and very small depth and area (Table 1), which might enable species to colonise the habitat. Moreover, this lake has never been strongly acidified (Fig. 2). Plešné Lake is mesotrophic, thus, likely offering better conditions for invertebrate survival.

In stream habitats (inlets and outlets), 237 species/taxa (64%) were found in total. Of these, Chironomidae, Trichoptera, and Plecoptera comprised the highest species number (151 taxa/species). Though the total number of inlet/outlet species is higher than that of lakes, one should keep in mind that more than 100 species/taxa occurring either in inlets or outlets (or in both) have been collected in the lakes as well (Tables 4, 5). Lake outlets (186) were more species-rich than inlets (123), despite the higher number of inlets studied. However, species composition of outlets might be strongly influenced by drift of larvae as well as imagines (Heteroptera, Coleoptera) from the lake. This can be documented, for example, by the occurrence of 8 species of Odonata or 4 species of Heteroptera found in outlets, the larvae of which develop solely in standing waters. The numbers of species/taxa recorded in running water habitats are partially influenced by the sampling effort. The outlets of Čerto-

vo Lake (72) and Laka Lake (99) exhibiting the highest numbers of taxa/species (Tables 4, 5) have been studied in detail by SVOBODOVÁ (2010) and SVOBODOVÁ et al. (2012), which probably resulted in higher numbers of recorded species. On the other hand, these outlets have higher discharge and channel width than other outlets, therefore they offer higher habitat heterogeneity and space for macroinvertebrates, which can lead to higher species diversity. Small outlets with relatively uniform substrate and low organic matter input hosted lower number of species (outlets of Černé Lake and Rachelsee).

The species richness of inlets seems to be quite heterogeneous and differences among the individual lakes (Table 5) are difficult to interpret. Though different number (1–3) of inlets was studied at each lake, it did not affect total species richness. For instance, three inlets were studied in Čertovo Lake and Rachelsee that hosted very different number of species (53 and 23, respectively). These differences might be explained by different acidity of inlets even of the same lake, so that the increase in number of the inlets studied need not increase total species richness. For instance, two distinct inlets of Laka Lake were studied – an acid one (pH ~5) was extremely species species-poor, while the other was near-neutral (pH ~6; KOPÁČEK, unpubl. data) and hosted most of the 55 species found in total. Moreover, the influence of water quality is combined with the size, slope, and discharge of an inlet. Thus, habitat-heterogeneous epirhithral streams need not necessarily host more species than very small crenal trickles.

The proportion of aquatic insects within aquatic invertebrate fauna

The fauna of aquatic insects represent a crucial part of the whole biota occurring in the Bohemian Forest lakes, including vertebrates and plants; however, the proper number of all taxa is still not precisely known. The dominance of aquatic insects can be roughly estimated reaching at least 60–75% of the whole taxa diversity of the lakes. More exact estimation can be presented taking into account only a single “ecological” group of biota, namely benthic and planktonic invertebrates.

Altogether 373 aquatic insect taxa recorded in the lakes exhibit about 9% of all aquatic invertebrates known from the Czech Republic and about 11% of all predominantly benthic aquatic invertebrates (cf. KUBÍČEK & VAŇHARA 1999). Insect aquatic fauna of the Bohemian Forest lakes reached 17.5% of approximately 2208 species of all aquatic insects of nine orders (except Hymenoptera) known from the Czech Republic (ROZKOŠNÝ & VAŇHARA 2004, BOUKAL et al. 2007, MALENOVSKÝ et al. 2012). This percentage seems to be considerably high taking into account that the studied area is small and only three aquatic habitats are present (lake littoral, crenal and rhithral streams). In much larger areas of the Czech Republic, which were studied in detail, this proportion was naturally higher reaching about 60% – e.g., the Pálava Biosphere Reserve (OPRAVILOVÁ et al. 1999), the Kokořínsko Protected Landscape Area (BERAN 2006), and the Bílé Karpaty Protected Landscape Area (MALENOVSKÝ et al. 2012).

Higher insect taxa

Altogether eight “true” insect orders (Hexapoda, Insecta *sensu stricto*) have been found in the Bohemian Forest lakes and their inlets/outlets (Table 4). This number reaches about a third of all insect orders present within the Czech Republic.

Some genera of ceryllids and grasshoppers (Orthoptera) live in emerged vegetation of some, mostly standing waters but no such representatives have been found in the Bohemian Forest lakes. The nearest localities of such species (e.g., the genus *Tetrix*, Tetrigidae) are distributed in the Bohemian Forest foothills (DOBŠÍK 1959). Thus, occurrence of some representatives of Hymenoptera in the Bohemian Forest lakes seems to be likely. These species

are either egg or larval parasitoids of a large scale of hosts currently present in the lakes and their inlets/outlets, e.g., the eggs of Diptera and Coleoptera are parasitised very frequently. There are about 10–12 families of both infraorders Terebrantia and Aculeata attacking aquatic insect hosts. The representatives of Agriotypidae, Mymaridae, Trichogrammatidae, and Scelionidae are most probably present in the Bohemian Forest lakes but escape our attention since their sampling requires specialised techniques and/or study of host eggs (cf. HEDQIST 1978, ROZKOŠNÝ 1980). A single representative of Agriotypidae (*Agriotypus armatus* Curtis, 1832) parasitises larvae of caddisflies of the family Goeridae (*Goera*, *Silo*, *Lithax*) and rarely the genus *Odontocerum* (family Odontoceridae) (KLAPÁLEK 1889a,b, ROZKOŠNÝ 1980). Only the latter host has been collected in the Bohemian Forest lakes but no larvae were observed parasitised (agriotypised, i.e. showing conspicuous breathing cord). Some representatives of the family Mymaridae have been detected in the Bohemian Forest but usually at localities below 750 m a.s.l. (PAPÁČEK & SOLDÁN 2003). They attack the eggs of diving beetles (Dytiscidae: *Dytiscus*, *Ilybius*) and damselflies (Odonata: Zygoptera), i.e. the hosts currently living also in the Bohemian Forest lakes. Similarly, numerous hosts of egg parasitoids of the families Trichogrammatidae and Scelionidae are abundant in the lakes. The former attack a large scale of hosts – Odonata: Zygoptera, Megaloptera (*Sialis*), Heteroptera: Nepomorpha (e.g., *Nepa*), Diptera (e.g., *Chrysops*, *Tabanus*), and Coleoptera (e.g., *Dytiscus*, *Donacia*), the latter develop in the eggs of Heteroptera: Nepomorpha and Gerromorpha (e.g., *Nepa*, *Gerris*).

Lepidoptera represent the only “true” aquatic insect order most probably not present in the Bohemian Forest lakes, neither are historical data on their occurrence. While the host plants of their caterpillars (*Elodea*, *Ceratophyllum*, *Potamogeton*, or *Stratiotes*) are locally abundant within most of the lakes, we never find them; neither imagines were ever attracted to light traps exposed several times at Prášilské Lake (SPITZER & JAROŠ, unpubl.). The Bohemian Forest lakes are likely situated above an altitudinal range of all aquatic Lepidoptera species. Yet representatives of the family Crambidae, subfamily Acentropinae (*Acentria ephemerella* (Denis & Schiffermüller, 1775), *Nymphula*, and *Parapoynx*) have been found at lower altitudes (approximately up to 650–700 m a.s.l.) in the Czech part of the Bohemian Forest (cf. PAPÁČEK & SOLDÁN 2003).

Among the insects *sensu lato*, only the class Collembola (springtails) exhibits aquatic (or rather semiaquatic) representatives. Number of aquatic springtail species is insufficiently known, about 30–35 species of 10–12 genera occurs in Europe (cf. GISIN 1978). Two taxa have been observed or collected in the Bohemian Forest lakes. A dense association of *Podura aquatica* Linnaeus, 1758 (order Arthropleona, family Poduridae) was observed in Laka Lake near the mouth of a “neutral” inlet (May 30, 2005), less numerous populations occurred in Plešné Lake among emerged aquatic plants near outlet (July 15, 1987, T. Soldán leg., M. Zacharda det.). Several specimens of *Sminthurides* cf. *aquaticus* (Bourlet, 1843) (order Arthropleona, family Sminthuridae) were collected in Grosser Arbersee (May 2002, M. Jezberová leg., M. Zacharda det.). Both species are widely distributed but their altitudinal range remains unclear; *Podura aquatica* seems to prefer lower altitudes. A temporal (or incidental) or permanent occurrence of springtails in the Bohemian Forest lakes remains open. The above findings seem to be unique, despite an effort to find any more specimens.

#### Notes to some records on non-insects fauna

Although our research has not been oriented to non-insects groups, we feel that several findings deserve a short comment since they often represent one of the first-time records in the lakes studied and the signs of biological recovery from acid stress. Non-insect groups of macroinvertebrates of the Bohemian Forest lakes are extremely poorly known as the only

earlier data were obtained by FRIČ & VÁVRA (1897). These species are hardly identifiable, because mostly invalid nomenclature has been used and the material has been lost.

**Mollusca** – Several specimens of *Pisidium* sp. were observed in Grosser Arbersee in 1998 (SOLDÁN, unpubl.) and Kleiner Arbersee in 2002 (JEZBEROVÁ, unpubl.). *Pisidium casertanum* (Poli, 1791) (Sphaeridae, Heterodonta, Bivalvia) was found in the littoral of Laka Lake and Grosser Arbersee (UNGERMANOVÁ 2009) and in a neutral inlet and outlet of Laka Lake (SENOO 2009). Its highest abundance (10 specimens of different age) has been observed in Laka Lake in 2010, some 5–10 m from the banks among submerged vegetation (SOLDÁN, unpubl.). Calcium concentration and pH are the main factors determining the occurrence of pea clams, which are sensitive to acidification – the majority of species disappear in pH <6.0, while even tolerant species disappear in pH <5 (ØKLAND & KUIPER 1982, HORSÁK & HÁJEK 2003). *P. casertanum* is the only species of the genus, which has been recorded even in some strongly acidified lakes – only a very few specimens could then be found and their shells were nearly completely decalcified (ØKLAND & KUIPER 1982). The occurrence of *P. casertanum* in the Bohemian Forest lakes is similar – the specimens have been found only in the recovering lakes (and inlets).

**Annelida** – A single species of a leech (Hirudinida, Glossiphoniidae) of the 24 species occurring in the Czech Republic (SCHENKOVÁ et al. 2009), namely *Helobdella stagnalis* (Linnaeus, 1758) was found in Grosser Arbersee and its outlet (UNGERMANOVÁ 2009, SENOO 2009) and in Laka Lake in 2010 (SYCHRA, unpubl.). Although it is a very common species in the Czech Republic (especially in stagnant and slowly flowing, mostly eutrophic waters), it is absent in streams above 800 m a.s.l. (SCHENKOVÁ et al. 2009). Thus, the Bohemian Forest lakes are the highest localities where the species has been found up to now.

**Amphipoda** – A single species of the order Amphipoda of the 9 species recorded from the Czech Republic (BEREZINA & ĎURIŠ 2008; ĎURIŠOVÁ et al. 2012), namely *Gammarus fossarum* Koch, 1835 was found in a semiquantitative sample from the littoral of Grosser Arbersee collected by a hand net in 2010 (SYCHRA, unpubl.). This is the first finding of this species in the Bohemian Forest lakes. This species is very abundant in clear streams. Its occurrence in a lake is rather unusual and specimens collected in standing waters are usually drifted from inlets. In the Bohemian Forest lakes, however, no specimens have been ever found in all inlets, neither in semiquantitative samples nor individually. The absence of the species is caused by unfavourable stream water chemistry, thus it occurs only in the outlet of Laka Lake (SVOBODOVÁ et al. 2012).

### **Mayflies (Ephemeroptera) – T. Soldán**

Species richness of mayfly taxocenoses

Altogether 19 species of 10 genera (14 subgenera) and 6 families (9 subfamilies) have been found in the Bohemian Forest lakes and their inlets and outlets (Tables 4, 6). One additional taxon, *Cloë* sp. recorded by FRIČ & VÁVRA (1897), cannot be determined at species level with certainty, because earlier authors used indiscriminately this generic name for species of genera *Cloeon* Leach, 1815, *Baetis* Leach, 1815, and *Procloeon* Bengtsson, 1915 (cf. BAUER-NFEIND & SOLDÁN 2012). Most probably, *Cloë* sp. might in fact represent *Cloeon dipterum*, for which the name used was frequently applied. Proper determination of *Ecdyonurus* cf. *austriacus*, reported sub. *E. picteti* (Meyer-Dür, 1864) by SVOBODOVÁ (2010), remains still unclear. Most morphological characters are closely related to *E. austriacus* Kimmins, 1958 described from the Austrian Alps, but careful comparison of type material and more material of imagines are necessary (cf. SOLDÁN 2003, SOLDÁN & GODUNKO 2006, SOLDÁN et al. 2008). Moreover, young larvae cannot be reliably distinguished from syntopic *E. silvaegabretae*.

The number of 19 species found in the Bohemian Forest lakes and their inlets/outlets represents approximately 18% of the total species diversity of Ephemeroptera in the Czech Republic, at present reaching 107 species in 30 genera and 16 families (ZAHŘÁDKOVÁ et al. 2009), and approximately 28% of 69 species of Ephemeroptera known from the Bohemian Forest and its foothills (cf. LANDA & SOLDÁN 1982, SOLDÁN et al. 2001).

#### Habitat preference and vagility of mayflies

A relatively low number of recorded species in comparison with other aquatic insect groups (Table 4) corresponds to general habitat specialisation of mayflies. Most species prefer streams of rhithral (all zones) and potamal (mostly epipotamal). Just inlets and outlets are inhabited by the majority of mayflies found in the Bohemian Forest lakes. Of 19 species found in total, only eight species (*Ameletus inopinatus*, *Siphonurus lacustris*, *S. alternatus*, *Cloeon dipterum*, *Baetis vernus*, *Leptophlebia marginata*, *L. vespertina*) are able to finish their development in the littoral zone of lakes. Others are specialised on habitats of running waters and might occur in the lakes only incidentally. For instance, of 13 species found in Laka Lake, 5 species were collected only in the inlets (1) and outlet (4); in Grosser Arbersee (11 species), 7 lived only in the outlet, 1 species only in the inlet (Table 6). There were no substantial differences between Czech and German lakes despite lesser attention that has been paid to German lakes in the past (SCHÖLL 1989, SCHAUMBURG 2000). Contrary to all lake outlets inhabited by 2–8 species, lake inlets are very poor in mayfly species. Mayflies were absent in the inlets of Čertovo Lake and Kleiner Arbersee. Inlets often represent a crenal habitat or transitory crenal-epirhithral zone only exceptionally inhabited by mayfly larvae. Taking into account the relatively very low vagility of mayflies, the lake water body might be a barrier preventing outlet–inlet species exchange at least in large lakes. Females emerged from the lakes, however, realise their compensatory flight into inlet habitats but larvae of most species cannot survive. Inlets are regularly inhabited by larvae of *Leptophlebia vespertina* and sometimes by those of *Ameletus inopinatus* but an active migration of larvae of the former species cannot be excluded. LINGDELL & MÜLLER (1979) observed migrations of older larvae towards estuarine habitats in coastal streams in Scandinavia.

#### Life strategies of *Leptophlebia* species

The most frequent species in each lake is *Leptophlebia vespertina* that occur in the littoral and outlets of all lakes and in most inlets (except for Grosser Arbersee and Kleiner Arbersee). Larvae are not specialised as to habitat requirements and are able even to survive longterm winter conditions close to anoxia (BRITTAIN & NAGELL 1981). They live among emerged vegetation, roots of sedges but also on stony substrates, on silt and woody debris. They are very rare on sandy substrata without organic debris. In Černé and Čertovo lakes, they live predominantly on compact rock or stony substrate but their densities are evidently higher at places rich in woody and organic debris. In other lakes, larvae apparently prefer emerged plants to plant-free bottom substrate. In Prášílské and Plešné lakes, their density can be roughly estimated to about 30–50 ind.m<sup>-2</sup> at stony substrate but about 100–150 ind.m<sup>-2</sup> at places overgrown with aquatic plants. The lowest density can be estimated in Černé Lake and especially Čertovo Lake (<20–30 ind.m<sup>-2</sup>). Density of larvae substantially decreased to ~10 ind.m<sup>-2</sup> at the depths of ca. 80–100 cm in all lakes. The transitory littoral–profundal zone seems to be free of larvae. On the contrary, the larvae may currently live at the depth of 5 m in some Norwegian lakes, even reaching densities of 70–665 ind.m<sup>-2</sup> (RADDUM & FJELLHEIM 1995). Densities of larvae in the Bohemian Forest lakes are comparable to those studied in Norway (usually 35–350 ind.m<sup>-2</sup>, but up to 1295 ind.m<sup>-2</sup> in some limed lakes).

**Table 6.** Species/taxa of mayflies (Ephemeroptera) found in the Bohemian Forest lakes in 1897–2010. Species collected in the lakes (see Table 1 for their codes) are in bold; occurrence in individual habitats is distinguished by findings in a lake (L), its inlets (I) and outlet (O); references to unpublished records are not in small caps, i.e., refer to the collector(s) and the year of finding(s).

Family / Species	CN	CT	PL	PR	LA	GA	KA	RA	References
<b>Ameletidae</b>									
<i>Ameletus inopinatus</i> Eaton, 1887	L, O		L	L	I	I			the 1950s (LANDA & SOLDÁN 1989) Soldán 2002, 2009 Chvojka 2007 UNGERMANOVÁ 2009
<b>Siphonuridae</b>									
<i>Siphonurus (Siphonurus) aestivatis</i> Eaton, 1903					L				Soldán 2010
<i>Siphonurus (Siphonurus) lacustris</i> Eaton, 1870		L	L	L	L	L			the 1950s (LANDA & SOLDÁN 1989)
			L	L	L	L			Soldán 1985, 1986, 1998, 1999
	L		L	L	L	L			Soldán 2002, 2006, 2009
					L				Chvojka 2007
					L				UNGERMANOVÁ 2009
<i>Siphonurus (Siphonurella) alternatus</i> (Say, 1829)				L					the 1950s (LANDA & SOLDÁN 1989) Soldán 2002, 2009
<b>Baetidae</b>									
<i>Cloë</i>	L								FRÍČ & VAVRA 1897
<i>Cloeon dipterum</i> (Linnaeus, 1761)	L				L	L			Soldán 2002, 2009 UNGERMANOVÁ 2009
<i>Baetis (Baetis) alpinus</i> (Pictet, 1843)	I	O				O		O	the 1950s (LANDA & SOLDÁN 1989) Soldán 2006, 2009
<i>Baetis (Baetis) vernus</i> Curtis, 1834						O		O	Soldán 2006, 2009 Jezberová 2002
<i>Baetis (Nigrobaetis) muticus</i> (Linnaeus, 1758)				O	L, O			O	Soldán 2009
<i>Baetis (Rhodobaetis) rhodani</i> (Pictet, 1843)					L, O				UNGERMANOVÁ 2009; SVOBODOVÁ 2010
<b>Heptageniidae</b>									
<i>Ecdyonurus cf. austriacus</i> Kimmins, 1958		O							Soldán 2006
<i>Ecdyonurus sphaegabretae</i> Soldán et Godunko, 2006					O				SVOBODOVÁ 2010
<i>Rhithrogena tridina</i> (Kolenati, 1839)					O			O	Soldán 2010
<i>Rhithrogena tovolaea</i> Navás, 1922					I				Chvojka 2007
					O				Soldán 2010

Table 6. Continued

Family / Species	CN	CT	PL	PR	LA	GA	KA	RA	References
<b>Leptophlebiidae</b>									
<i>Leptophlebia marginata</i> (Linne, 1767)					L				Chvojka 2007
					L,O				UNGERMANOVÁ 2009; SVOBODOVÁ 2010
<i>Leptophlebia vespertina</i> (Linnaeus, 1746)	L	L,O	L	L	L				the 1950s (LANDA & SOLDÁN 1989)
	L	L	L	L	L	L	L	L	Soldán 1985, 1986, 1989, 1990, 1998, 1999
		L		L					SOLDÁN et al. 1998, 1999
								L	SCHÖLL 1989
I,L		L,O			L,O				Jezberová 2002
L	L	L		L		L	L	L	Soldán 2002, 2006
I,L,O	I,L,O	I,L,O	I,L,O	I,L,O	L,O	L,O	L,O	I,L,O	SENGO 2009; UNGERMANOVÁ 2009; SVOBODOVÁ 2010
<i>Habroleptoides confusa</i> Sartori et Jacob, 1986						O	O		Soldán 2010
<i>Habroplebia lauta</i> Eaton, 1984	O				O				SVOBODOVÁ 2010; Soldán 2010
<b>Ephemerellidae</b>									
<i>Ephemerella ignita</i> (Poda, 1761)						O			Soldán 2010
<i>Ephemerella mucronata</i> (Bengtsson, 1909)					O	O			Soldán 2010
<b>Total number of species</b>	<b>7</b>	<b>4</b>	<b>4</b>	<b>5</b>	<b>13</b>	<b>11</b>	<b>3</b>	<b>5</b>	
Number of species in lakes	5	2	4	4	8	3	1	1	
Number of species in outlets	3	3	1	2	8	8	3	5	
Number of species in inlets	2	1	1	1	2	1	0	1	
Number of species in inlets and outlets	4	3	1	2	9	9	3	5	

*Leptophlebia vespertina* possesses life cycle of the univoltine winter type characterised by presence of larvae at the localities from late summer to next late spring (LANDA 1968, SOWA 1975b, CLIFFORD 1982). Due to its embryogenesis, larvae are missing in habitats from mid June till late August, when only a very small (body length of 2–3 mm) larvae can be found. During winter, larval development is nearly ceased. Larval growth became intensive again after ice cover melting and warming of water in spring (MOON 1938, SÆTTEM & BRITTAİN 1985, KIEL & MATZKE 2002) and its rate is highest during the first three months after hatching (KJELLBERG 1972, BRITTAİN 1974, 1978, SAVAGE 1986, SÖDERSTRÖM 1991). Emergence has been observed either from stones and other emerged subjects (cf. SCHOENEMUND 1930b, TIENSUU 1935) or from the water surface (cf. KJELLBERG 1972, 1973). Both ways of emergence have been observed in the Bohemian Forest lakes. Larvae mostly emerge from the water surface at places with stony bottom and minimal vegetation cover (Černé, Čertovo, and Prášílské lakes), while, in lakes with the littoral rich in vegetation (Laka Lake and Kleiner Arbersee), they evidently prefer emerging from emerged plants and only about 10–20% of them emerge from the water surface. Under laboratory conditions, however, about 70% of 415 individuals emerged from stone surface (SOLDÁN, unpubl.). Subimagines usually emerge around noon, especially at the localities of lower altitude (as in *L. marginata*), but the emergence lasting all day long (approximately from 9:00 a.m. to 3:30 p.m.) has been observed in the Bohemian Forest lakes (e.g., in Černé and Prášílské) like in some other higher altitude localities (cf. LANDA 1969, SOLDÁN & ZAHŘÁDKOVÁ 2000). Contrary to *L. marginata*, subimagines usually do not fly at all and remain sitting among vegetation and stones near water surface; subimaginal stage lasts about 24 hours. Mating flight occurs in the afternoon (usually from 1:00 to 4:00 p.m.). Swarming in early evening or at dusk after sunset that was observed at lower altitudes (cf. SAVAGE 1986, FONTAINE et al. 1990, HAYBACH 1998) has never been observed in the Bohemian Forest lakes. The imagines usually do not search for any conspicuous landmarks or swarm markers such as limited areas of homogenous vegetation, a rock, bush, tree, light-coloured object (cf. SAVOLAINEN 1978). They swarm mostly above the shore line or a bridge or road surface at a height of approximately 1–2.5 m preferring bright sky and often sunny places to cloudy moments or shadowed places in the Bohemian Forest lakes (observed at the shore of Černé Lake in May 2007). Swarms of *L. vespertina* are relatively small, up to 10–15 individuals. Pronounced and apparently directed compensatory flight of females has not been observed and probably does not occur in the Bohemian Forest lakes (surveyed in Kleiner Arbersee, Černé, Čertovo, and Prášílské lakes in 2005–2007).

The emergence period of *L. vespertina* apparently showed little different timing. It was rather controlled by lake morphology (more rapid temperature rise in shallow lakes in spring) than by the altitude. Subimagines were observed to start emergence in mid May and to finish as late as in early June in shallow Laka Lake (highest altitude), while the emergence started in late May and lasted ~10 days in Černé Lake. Similar timing was observed in Prášílské Lake. The latest emergence, with an apparent peak in the first half of June was observed in Čertovo Lake.

Successful colonisation of lakes by *Leptophlebia vespertina* is due to convenient life cycle strategies that enables to develop simultaneously with the second most abundant species, *Siphonurus lacustris*, coexisting in the same lake littoral habitats as studied in detail in Norwegian lake Myrkdalsvatn and Øvre Heimdalsvatn (BRITTAİN 1978, 1980, SÆTTEM & BRITTAİN 1993). Strategy in *Leptophlebia vespertina* consists of small body size (in Norwegian lakes 7.1–8.7 mm), high density, main larval growth during late summer and autumn, a short emergence during mid-summer and low fecundity (645–1079 eggs per female in oligotrophic Norwegian subalpine lakes) and low mortality (365–461 eggs required to produce one subimago). These values are not the same but comparable within the Bohemian Forest

lakes. Body length is a little higher (7.6–9.3 mm within all the lakes) and the fecundity seems to be apparently lower (490–935 and 365–702 egg per female in Černé and Čertovo lakes in the 1990s; SOLDÁN, unpubl.). Mortality was not studied. Strategy of *Siphonurus lacustris* consists of large body size (11.5–13.2 mm), low density (compared to *L. vespertina*), main larval growth between ice-break and emergence (thus partly utilising a free niche, when *L. vespertina* is in egg stage), a long emergence period during autumn and summer (or possible bivoltine life cycle, see below), high fecundity (1575–1740 eggs per female), and high mortality (720–931 eggs necessary to produce one subimago). These strategies seem to be influenced by interspecific competition and coexistence of *L. vespertina* and *S. lacustris* (or *S. aestivalis*), and appear to have been established by ecological segregation through natural selection (ULFSTRAND 1968).

Larvae of *Leptophlebia marginata* has been found only in Laka Lake (Table 6). Although this occurrence can be considered incidental, the species apparently reproduce here as documented by finding of imagines during sweeping of littoral vegetation (CHOVKA, unpubl.). The species is abundant and widely distributed within the Czech Republic but prefers lower altitudes (up to ca. 650 m); its occurrence above 1000 m a.s.l. is quite exceptional and hitherto documented only from Norway (up to 1800 m, BRITAIN 1979). *L. marginata* is often syntopic with *L. vespertina*, density of larvae apparently decrease with increasing altitude in favour of *L. vespertina* in central Europe (cf. LANDA 1969, LANDA & SOLDÁN 1989, SOLDÁN et al. 1998). This is documented, for example, by the proportion of *L. marginata* of all *Leptophlebia* specimens (80–90%) at some other localities of the Bohemian Forest (e.g., pools in the floodplain of the Vltava River near Pěkná). Its life cycle is of the univoltine winter type (details about life cycle and growth in SÖDERSTRÖM 1991, BRITAIN 1976, SAVAGE 1986). Growth of larvae is more rapid before emergence than in *L. vespertina* (cf. BRITAIN 1974, 1978, 1980, BRITAIN & LILLEHAMMER 1978). Subimagines emerge around noon and, contrary to *L. vespertina*, actively fly toward trees and shrubs. If syntopic with *L. vespertina*, *L. marginata* begins its mating flight earlier, frequently during daylight before sunset. On the contrary, *L. marginata* shows bimodal swarm activity in the beginning of the flight period while unimodal swarming activity has been observed at the peak of the flight period (SAVOLAINEN 1978).

#### Life strategies of *Siphonurus* species

Larvae of *S. lacustris*, the second most abundant species in the Bohemian Forest lakes, occur in rivers, stream pools and lakes, at altitudes from ca. 500 m a.s.l. upwards (up to 2300 m a.s.l. in Switzerland, SARTORI & LANDOLT 1999). Macrophytes are preferred, but larvae live on submerged roots and mosses. Their occurrence on a stony bottom or the bottom covered with organic debris is rare. Due to an evidently larger ecological range (certain eurythermy and wide habitat preference), the larvae are able to colonise new habitats very quickly and to reach even mass population density, e.g., in new montane reservoirs (SOLDÁN et al. 1998). The species is at mostly moderately abundant in the Bohemian Forest lakes. Generally, a univoltine cycle of *S. lacustris* is supposed, a discussion mainly concerns either egg or larval overwintering. While LANDA (1968, 1969) supposed the egg winter quiescence in the Czech Republic, most authors (e.g., BRITAIN 1974, 1978, 1980, SÆTTEM & BRITAIN 1985, 1993, SOWA 1975b) observed egg hatch in autumn and, consequently, younger larvae to overwinter in lake populations in Norway, Great Britain, and south Poland. BRITAIN (1978) pointed out that both life cycle strategies (either egg or larval overwintering) were possible within the same population, although he did not manage to determine the proportion of overwintering eggs and young larvae. LANDA (1968, 1969) described a second, summer-autumn generation in some populations in the Czech Republic, which occurred only under exceptionally favour-

rable water temperature conditions at lower altitude. We have observed relatively numerous second generations of *S. lacustris* with flight period in August and September at several localities of the Sudetes in 1973, 1976, 1995, and 2000 (SOLDÁN et al. 1998, SOLDÁN & ZAHRÁDKOVÁ 2000). Although no exact data are available, growth of population in the Bohemian Forest (and most likely also in the lakes) is concentrated mostly to spring months (April to June), development of overwintering larvae is very inconspicuous or ceased, imagines were observed flying from late May to mid July. Some imagines that might belong to the second generation were collected by sweeping in September (SOLDÁN, unpubl.).

*Siphonurus alternatus* has been collected in three lakes (Laka, Plešné, Prášílské). The species shows a distribution indicating north-central European disjunction (LANDA 1954, 1969, SOWA 1975a, LANDA & SOLDÁN 1985). Larvae prefer rather lentic habitats, especially pools with submerged vegetation, from isolated backwaters of large rivers to oligotrophic (or mesotrophic) ponds and artificial impoundments, as well as montane and submontane glacial lakes, but are able to colonise brackish aquatic habitat too (e.g., in Scandinavia and Estonia). Within the Czech Republic, they generally live at places with very slow current velocity (typically in backwaters of larger rivers) or oligotrophic ponds and impoundments of the colline zone (e.g., the Lužnice River basin or fishponds around Lnáře and Blatná). They can reach relatively high population densities especially after the end of emergence of other *Siphonurus* species and the first generation of *Cloeon dipterum* (cf. SOLDÁN & ZAHRÁDKOVÁ 2000). Within the Bohemian Forest lakes, larvae are always solitary to rare, being collected individually at littoral places densely overgrown with aquatic vegetation. The life cycle of *S. alternatus* is usually considered the seasonal univoltine summer (spring-summer) type (Us according to CLIFFORD 1982) as observed in the Bohemian Forest lakes and generally within the whole central Europe (cf. LANDA 1954, 1968, ZAHRÁDKOVÁ et al. 2009). After oviposition in early summer, the eggs are supposed to hatch from next May to June after winter and spring quiescence. In the Bohemian Forest lakes, its flight period (judging from the occurrence of penultimate and ultimate larval stages) is a little postponed to the very end of May and mid June, most probably due to later ice melting in April. However, we have collected imagines by sweeping in Laka Lake as late as in late September in 2010. This might indicate a possibility of the second generation, more likely than extremely prolonged flight period.

Contrary to the lakes in Fennoscandia, another representative of the genus, *S. aestivalis* is very rare in the Bohemian Forest. Larvae were found only in Laka Lake and incidental upstream migration cannot be excluded in this case. At lower altitude, if the larvae are syntopic with *S. lacustris*, their abundance conspicuously increases with decreasing altitude (e.g., at numerous localities in the Bohemian Forest foothills). The life cycle is approximately of the same type as in *S. lacustris*. Life cycle strategy enables *S. aestivalis* to coexist successively with *L. vespertina* and *S. lacustris*. At least in Scandinavia, *S. aestivalis* shows large body size, very low density, main larval growth during winter and spring (in between *S. lacustris* and *L. vespertina*), high fecundity (about 1000–1800 eggs per female) and relatively high mortality (BRETSCHKO 1985, 1990, SARTORI et al. 1991, 1992, SÆTTEM & BRITAIN 1993).

#### Other species of the lakes

*Ameletus inopinatus* has been found in three lakes (Černé, Prášílské, Plešné). Its larvae are stenoxymbiotic and cold stenothermic, thus, they inhabit creanal and epirhithral running waters with stony bottom at higher altitudes (or colder climate) and the shore zone of lakes. They are solitary to very rare, clearly preferring stony parts of the littoral zones in the Bohemian Forest lakes. If they occur in epirhithral habitats (e.g., inlets), they inhabit also places with roots and organic debris and submerged vegetation at current-exposed places (e.g., in Grosser Arbersee). Subimagines emerge on plants and stones just above the water surface

during daytime. Swarming and copulation may take place at considerable height in the air. Most authors (e.g., LANDA 1968, 1969, BRITAIN 1978, 1979, SOWA 1975b) report for *A. inopinatus* an entirely univoltine winter life cycle type (CLIFFORD 1982). GLEDHILL (1959) observed a part of eggs remaining in winter dormancy and hatching very early in spring. Such larvae give rise to apparently smaller adults flying a bit later than those emerging from overwintering larvae, indicating that obligatory diapause does not take place. This has also been documented in the continental Europe (e.g., in the Thuringian Forest, BRETTFELD 1990), indicating a seasonal, univoltine winter-summer life cycle (LANDA 1968, 1969, SOWA 1975b, CLIFFORD 1982). The same alternative life cycle can be supposed also in the Czech Republic, most likely including the Bohemian Forest lakes. Apparently two size groups of larvae are regularly observed, as well as smaller adults flying in late August and early September. “Normal” populations of *A. inopinatus* (rather the majority of population within the Czech Republic) exhibit flight period from late May to late June or early July (BAUERNFEIND & HUMPEŠCH 2001, ZAHŘÁDKOVÁ et al. 2009).

Larvae of the last “true” Bohemian Forest lakes inhabitant, *Cloeon dipterum* inhabit almost all types of aquatic habitats being sometimes eudominant, e.g., in eutrophicated fishponds, but they are recorded also from the rhithralic section of rivers tolerating current velocity up to  $0.6 \text{ m}\cdot\text{s}^{-1}$  (DORIER & VAILLANT 1954). An obviously preferred habitat is aquatic vegetation. *C. dipterum* represents a typical pioneer species colonising new localities (including astatic water bodies, SARTORI & LANDOLT 1999) and exhibits some attributes of invasive behaviour (LANDA & SOLDÁN 1986). Its life cycle is highly adaptive, a seasonal bivoltine winter cycle (MBWs) is usual. The minimum temperature of  $\sim 8^\circ\text{C}$  is necessary for successful metamorphosis (BRETSCHKO 1965, MCKEE & ATKINSON 2000) and temperature seems to be a major factor affecting population development. The findings of this species in the Bohemian Forest lakes (Černé, Laka, Grosser Abersee, Table 6) seem to be rather incidental and permanent dense populations, often observed in lowland ponds, definitively do not occur here. Colonisation of the lake habitats is enabled by extremely wide ecological range of larvae including food requirements (HAYBACH 1998, CIANCIARA 1979, 1980a,b), relatively rapid growth and development (although only a single generation can be supposed here), extreme vagility (ovoviviparous females living in imaginal stage for a long time, DEGRANGE 1959, 1960, SOLDÁN 1987, SILINA 1994), as well as survival of low oxygen concentrations or even anoxia (NAGELL 1977, 1981).

### Species of inlets and outlets

Distribution of the majority of mayfly species (*Baetis alpinus*, *B. vernus*, *B. muticus*, *B. rhodani*, *Ecdyonurus* cf. *austriacus*, *Rhithrogena iridina*, *Rh. loyolaea*) is restricted to outlets of the lakes, as well as an incidental occurrence of remaining species (*Ephemerella ignita*, *E. mucronata*, *Habrophlebia lauta*, *Habroleptoides modesta*). The only exception is the occurrence of larvae of *B. vernus* in Laka Lake (Table 6), while they live only in outlets in the other lakes (Prášílské Lake, Kleiner Arbersee). *B. vernus* is characterised by having a relatively large ecological range and moderate acid tolerance (BRAUKMANN 2001, TIXIER 2004). It is the only representative of the genus, which can colonise oligotrophic and mesotrophic stagnant waters (fishponds).

The outlets usually belong to the epirhithral zone, a habitat quite suitable for mayfly larvae. Mayfly fauna of these habitats consists of two components. Upper segments of the outlets studied (ca. 50 m) are inhabited by the species drifted from the lake, which become apparently less frequent downstream. This concerns predominantly “lake” species *L. vespertina* and *S. lacustris*, which show the highest densities at the very beginning of an outlet. The second group is upstream migrants that are much more abundant or common downstre-

am. Some of them, like *Baetis alpinus* and *B. rhodani*, are collected rather regularly. Others, like *Habrophlebia lauta*, *Habroleptoides confusa*, *Ephemerella mucronata*, and *E. ignita*, are extremely rare in the outlet segments studied (always a single larva was found). The more neutral outlets of Grosser Arbersee and Laka Lake are probably most suitable to upstream migration and survival of these species (cf. Table 6). Although downstream sections are densely inhabited by these species (e.g., *E. ignita* often belongs to eudominant species), this migration seems to be rather unsuccessful.

Lake inlets are inhabited only by four species, *Baetis alpinus*, *A. inopinatus*, *Leptophlebia vespertina*, and *Rhithrogena iridina*. The occurrence of these species in inlets seems to be rather exceptional, as documented, for example, by finding of a female of *Rh. iridina* collected by sweeping in an inlet of Laka Lake (Table 6).

#### Acid sensitivity and impact of acidification

Although mayflies are generally reported as one of the most acid-sensitive macroinvertebrates (SUTCLIFFE & CARRICK 1973, PETERSON et al. 1985, ØKLAND & ØKLAND 1986, LEPORI et al. 2003), the mayflies found in the Bohemian Forest lakes represent an exception. *Leptophlebia vespertina* is probably the most acid-tolerant mayfly at all (RADDUM et al. 1988, FJELLHEIM & RADDUM 1992, RADDUM & SKJELKVÅLE 1995). Its tolerance limit to survive is pH ~4.0 (ENGBLOM & LINGDELL 1983) and larvae can tolerate brackish waters with salinity of 4–5‰ and conductivity of 9 mS.cm<sup>-1</sup> (LINGDELL & MÜLLER 1979, MERILÄINEN 1988). However, the acid-stressed populations were significantly reduced in Norway (RADDUM & FJELLHEIM 1995). Likewise, this species survived strong acidification in the Bohemian Forest lakes in the past, yet its densities considerably dropped especially in Černé, Čertovo and Plešné lakes. For instance, larvae were extremely rare in Čertovo Lake already in 1956, when pH was as low as 4.7 (LANDA et al. 1984). In the early 1980s, some sampling did not even detect larvae at all. Their recent densities (estimated in 2002, 2007, and 2010) seem to be stable again.

*Ameletus inopinatus* and *Siphonurus lacustris* represent the only mayfly species that can tolerate periodic acidity (RADDUM et al. 1988, BRAUKMANN 2001) and their level of tolerance is pH >5.5. In the period of strong acidification (the late 1970s to mid-1980s), when pH of the Bohemian Forest lakes decreased below 5 (VESELÝ 1994, VRBA et al. 2000), both species apparently disappeared from strongly acidified lakes (*S. lacustris* from Čertovo and Plešné lakes, *A. inopinatus* from Plešné and Prášilské lakes). On the other hand, *S. lacustris* survived in Laka Lake, which exhibited more favourable conditions (usually pH >5, Fig. 2), during the whole period from the 1950s till present. *S. alternatus* (collected only in Prášilské Lake in the 1950s), which is believed to survive acid periods in spring in the egg stage (RADDUM & FJELLHEIM 1995), has appeared at new localities after 2000 (Table 6).

“True” acid-sensitive species (i.e. species usually found only in streams that are never acidic, BRAUKMANN 2001), such as *Ephemerella ignita*, *Habrophlebia lauta*, and *Habroleptoides confusa*, have been found in lake outlets quite incidentally and only recently, although they are widespread in the Bohemian Forest. A relatively acid-sensitive species *Baetis alpinus* could apparently survive, but only in inlets/outlets. Biological responses to the chemical recovery from acid stress in the Czech lakes can be documented by new occurrence of *A. inopinatus* and *S. lacustris* in Černé Lake and findings of further species (*Baetis vernus*, *Leptophlebia marginata*, *Rhithrogena iridina*, and *Ecdyonurus* cf. *austriacus*). Certain recovery can be inferred from findings of several species of the genus *Baetis*, generally considered acid-sensitive (inhabiting episodically weakly acidic streams, according to BRAUKMANN 2001), in outlets of the lakes. These species differ in degree of acid sensitivity (TIXIER et al. 2009) and their survival strongly depends on other factors, like toxic aluminium (RADDUM & FJELLHEIM 1987). While *B. rhodani* and *B. alpinus* are “slightly” acid-sensitive (cf.

BRADLEY & ORMEROD 2002, RADDUM & FJELLHEIM 2003), *B. vernus* belongs to “acid-benefiting” species, which increased their relative densities with increasing acidity (TIXIER et al. 2009). On the other hand “very” acid-sensitive species, e.g., *B. melanonyx* and *B. scambus* (TIXIER et al. 2009) still do not occur in inlets and outlet segments close to the lakes.

## **Dragonflies (Odonata) – T. Soldán & J. Bojková**

### Species richness of taxocenoses

Contrary to most other aquatic insects, Odonata occupy a rather unique position especially concerning their vagility and reproductive/distributional fitness. The imagines represent outstanding fliers, perhaps one of the most successful ones within the insects in general. Their wide vagility depends also on some features of their biology, such as feeding and foraging habits, mass migrations, invasive behaviour, and tendency to territoriality. Many species of wide ecological range tend to colonise also extreme and/or astatic aquatic habitats. Therefore, their findings as well as long-term occurrence in the Bohemian Forest lakes should be evaluated with caution. Some findings of imagines might represent incidental occurrence only, some findings of larvae might be due to facultative or even seasonal occurrence rather than permanent colonisation and survival of the whole population under unfavourable conditions in the lakes. On the other hand, numerous species permanently live in peat bogs or other habitats in a close vicinity of the lakes and some of them might colonise the lake littoral, yet still have escaped our attention.

Besides two species (*Ischnura* sp. and *Libellula* sp.) determined only at the generic level (too young larvae without critical distinguishing characters), altogether 20 species of 12 genera and 5 families of the suborders Zygoptera (Lestidae: 1 species, Coenagrionidae: 6 species) and Anisoptera (Aeshnidae: 6 species, Corduliidae: 2 species, Libellulidae: 6 species) have been so far collected in the lakes and their inlets and outlets (Tables 4, 7). This number represents a half (~54%) of the Odonata species diversity reaching as many as 37 species recorded from the Bohemian Forest within the Šumava Protected Landscape Area (SOLDÁN et al. 1996, CEMPÍREK 2000, ZELENÝ & HANEL 2000, ZELENÝ 2004a). Generally, the number of species found in the Bohemian Forest is high in comparison with other Hercynian mountains. For instance, in the Krkonoše (Giant) Mts., only 25 species have been found so far (HOLUŠA & VANĚK 2008).

The occurrence of dragonflies in the Bohemian Forest, which included findings in the close vicinity of the lakes, was mentioned by KREJČÍ (1890) for the first time. He probably collected imagines at least near Prášilské Lake; however, he did not provide any details on concrete localisation of his findings. Later, this author mentioned the occurrence of imagines of *Aeshna juncea* at Prášilské Lake, *Cordulegaster bidentata* Sélys, 1843, *Ae. affinis* Van der Linden, 1823, *Ae. grandis*, and *Somatochlora metallica* at Prášily (without precise localisation again, KREJČÍ 1892). Due to very close distance between the village of Prášily and Prášilské Lake, the occurrence of these species just at Prášilské Lake itself was very likely; however, the original material probably has not been preserved and revision remains impossible. Thus, these records remain doubtful, except for the latter two species that have been documented in other lakes (HOLUŠA 1996, 2000, and unpublished records in Table 7). Further record from the 1890s presented FRIČ & VÁVRA (1897), who determined larvae as “*Libellula*” in Černé Lake (the material was not preserved). Altogether 11 species were collected till the end of the last century. Besides a single record on *Leucorrhinia dubia* from Černé Lake by PERUTIK (1957), some data based solely on extensive collecting activities in early June and mid August 1987 were acquired from Plešné Lake (SOLDÁN, unpubl.). Five of 7 species collected at that time actually represented species recorded in the lakes for the first

**Table 7.** Species/taxa of dragonflies (Odonata) found in the Bohemian Forest lakes in 1892–2010. Species collected in the lakes (see Table 1 for their codes) are in bold; occurrence in individual habitats is distinguished to findings in a lake (L), its inlets (I) and outlet (O); references to unpublished records are not in small caps, i.e., refer to the collector(s) and the year of finding(s).

Family /Species	CN	CT	PL	PR	LA	GA	KA	RA	References
<b>Suborder Zygoptera</b>									
<b>Lestidae</b>									
<i>Lestes sponsa</i> (Hansemann, 1823)				L	L				HOLUŠA 2000 Jezberová 2002 Chvojka 2007
<b>Coenagrionidae</b>									
<i>Pyrrhosoma nymphula nymphula</i> (Sulzet, 1776)	L	L							Chvojka 1991 HOLUŠA 2000 Jezberová 2002 SENOO 2009 SYCHRA et al. 2008 Soldán 2010 Soldán 2009
<i>Coenagrion hastulatum</i> (Charpentier, 1825)			L,O			L	L	L	Soldán 2010 Jezberová 2002 Soldán 2010
<i>Coenagrion puella</i> (Linnaeus, 1758)						L,O			HOLUŠA 2000 Jezberová 2002 Soldán 2010
<i>Enallagma cyathigerum</i> (Charpentier, 1840)				L	L	L,O			HOLUŠA 2000 Jezberová 2002 Soldán 2010
<i>Ischnura elegans elegans</i> (Van der Linden, 1820)	L	L	L	L	L,O	L,O	L	L	SENOO 2009; UNGERMANOVÁ 2009 Soldán 1987 Soldán 1987 UNGERMANOVÁ 2009
<i>Ischnura pumilio</i> (Charpentier, 1826)			L						
<i>Ischnura</i> sp.	L								
<b>Suborder Anisoptera</b>									
<b>Aeshnidae</b>									
<i>Aeshna caerulea</i> (Ström, 1783)			L	L				L	UNGERMANOVÁ 2009 Soldán 1987
<i>Aeshna cyanea</i> (O.F. Müller, 1764)		L,O		L	L	L	L	L	HOLUŠA 2000 Jezberová 2002 Chvojka 2007 SENOO 2009; UNGERMANOVÁ 2009
<i>Aeshna grandis</i> (Linnaeus, 1758)	I,L,O	L	I,L,O	L	L	L	L,O	L	Soldán 2010 Soldán 1987

Table 7. Continued

Family / Species	CN	CT	PL	PR	LA	GA	KA	RA	References
<i>Aeshna juncea</i> (Linnaeus, 1758)				L					KREJČÍ 1892
						L		L	Jezberová 2002
<i>Aeshna subarctica elisabethae</i> Walker, 1908	L		L	L	L	L	L	L	Soldán 2010
<i>Aeshna viridis</i> Eversmann, 1836		O							Soldán 1987, 2002 SENOO 2009
<b>Corduliidae</b>									
<i>Cordulia aenea</i> (Linnaeus, 1758)							L,O		Jezberová 2002
						L			Soldán 2010
<i>Somatochlora metallica metallica</i> (Van der Linden, 1825)	L				L				HOLUŠA 1996, 2000
	L	L			L				SYCHRA et al. 2008
	L	L	L,O	L,O	I	L	L	L	SENOO 2009; UNGERMANOVÁ 2009
	L	L		L,O	L	L	L		Soldán 2010
<b>Libellulidae</b>									
<i>Libellula quadrimaculata</i> Linnaeus, 1758			L				L,O	L	Soldán 1987
									Soldán 2010
<i>Libellula</i> sp.	L								FRÍČ & VÁVRA 1897
							L		UNGERMANOVÁ 2009
						L			Soldán 2010
<i>Orithetrum cancellatum</i> (Linnaeus, 1758)			L						Soldán 1987
<i>Sympetrum danae</i> (Sulzer, 1776)							L		Chvojka 2007
<i>Sympetrum sanguineum</i> (Müller, 1764)						L			Soldán 2010
<i>Leucorrhinia dubia</i> (Van der Linden, 1824)	L								PERUTÍK 1957
	L								HOLUŠA 1996
							L		Soldán 2010
<b>Total number of species</b>	<b>8</b>	<b>5</b>	<b>11</b>	<b>8</b>	<b>6</b>	<b>12</b>	<b>10</b>	<b>8</b>	
Number of species in lakes	8	4	11	8	6	12	10	8	
Number of species in outlets	1	3	2	3	2	4	4	0	
Number of species in inlets	1	0	1	0	0	1	0	0	
Number of species in inlets and outlets	1	3	2	3	2	5	4	0	

time (*Ischnura pumilio*, *Aeshna cyanea*, *Ae. subarctica*, *Orthetrum cancellatum*, *Libellula quadrimaculata*). CHVOJKA (unpubl.) collected imagines of *Pyrrhosoma nymphula* in Čertovo Lake and HOLUŠA (1996, 2000) published the findings of *Lestes sponsa*, *Pyrrhosoma nymphula*, *Enallagma cyathigerum*, *Aeshna cyanea*, and *Somatochlora metallica* for the first time. The same author re-collected *Leucorrhinia dubia* in Černé Lake (HOLUŠA 1996). Additional 9 species have been found recently during the extensive survey of lake benthic entomofauna (Table 7). Except of a record on a single undetermined species of “*Libellula*”, the three German lakes were not studied with respect to Odonata till the beginning of this century. Eleven species have been found there so far (Table 7).

Species groups according to reproductive and colonisation strategies

Owing to extreme vagility, the species collected in the Bohemian Forest lakes can be divided into the following distinct groups:

(i) Species permanently living within the lake water bodies, i.e. repeatedly realising their complete life cycles there. This group can be documented by findings of larvae of different body size, in different years and/or seasons. In other words, the respective lake and/or its inlet/outlet habitats are suitable for completing growth and development of their larvae, and successful emergence. At least 11 species of 20 species collected in the lakes belong to this group. *Pyrrhosoma nymphula* and *Aeshna cyanea* are the most common species that have been found repeatedly in all the lakes. *Ischnura elegans*, *Somatochlora metallica*, and *Aeshna juncea* belong to frequent species found in six or five of all eight lakes. Other species, *Coenagrion hastulatum*, *C. puella*, *Enallagma cyathigerum*, *Cordulia aenea*, *Libellula quadrimaculata*, and *Leucorrhinia dubia*, were recorded from one to four lakes and their larvae were collected repeatedly in different seasons and/or years. *P. nymphula* and *Ae. cyanea* show wider ecological range by often inhabiting lake outlets (in five and four lakes, respectively), whereas some other species, such as *Coenagrion* spp., *E. cyathigerum*, *C. aenea*, *S. metallica*, and *L. quadrimaculata*, colonise lake outlets only exceptionally. Larvae of two species, *Ae. juncea* and *L. dubia*, were not found in lake outlets at all (Table 7). Inlets were nearly free of dragonflies; only eurytopic *Ae. cyanea* and *S. metallica* were found there. Inlets represent rather unsuitable habitat for dragonfly larvae due to lack of submerged vegetation, rough substrate, and relatively high current velocity. Their colonisation seems to be quite exceptional or, most likely, of temporal character.

(ii) Species able to colonise lakes but temporal character of colonisation cannot be excluded. Such species are probably not able to finish their complete life cycle or emergence and their survival to next generation seems to be restricted. Classification into the groups of individual species is rather tentative, since no regular sampling during one or several seasons is available and thus survival of larvae cannot be properly determined. Consequently, some species might actually belong to permanent but rare inhabitants of lakes as characterised in the former group. We assigned to this group *Sympetrum sanguineum*, which was collected in larval stage only once in Grosser Arbersee and imagines were neither collected nor observed. Further, *Lestes sponsa* were collected only once in larval stage in Prášílské Lake and in imaginal stage in Laka Lake and Grosser Arbersee. Larvae of *Aeshna caerulea* were found in Prášílské Lake and Rachelsee and incidentally in Plešné Lake in imaginal stage. *L. sponsa* and *S. sanguineum* belong to the most common species of Odonata within the Czech Republic. They represent eurytopic species inhabiting various types of standing waters (MERRITT et al. 1996, ASKEW 2004, DIJKSTRA & LEVINGTON 2006, DOLNÝ et al. 2007). They occur predominantly at lowland and colline localities, approximately 90% of findings in the Czech Republic refer to the altitude up to 600 m. a.s.l. (DOLNÝ et al. 2007). The occurrence of larvae above 1000 m in montane glacial lakes is quite incidental and long-term survival

of their populations can be limited. In contrast, *A. caerulea* is a stenotopic species known from three isolated montane areas within the Czech Republic at the altitudes of 1025–1135 m a.s.l., which include the Bohemian Forest (DOLNÝ et al. 2007). Its larvae live in small water bodies of the area 5–50 m<sup>2</sup> and pools in peat bogs and prefer open and insolated places sparsely overgrown with *Pinus mugo* (DOLNÝ et al. 2007). Such habitats are obviously missing in the vicinity of Rachelsee, Prášílské, and Plešné lakes.

(iii) Species collected only in imaginal stage that probably do not reproduce and oviposit in the Bohemian Forest lakes. Their occurrence is incidental being apparently related to some type of migration or foraging. Five species can be ranked within this group of species: *Ischnura pumilio*, *Aeshna grandis*, *Ae. subarctica*, *Orthetrum cancellatum*, and *Sympetrum danae* (Table 7). Most of them are not able to reproduce, survive and even to oviposit, because of a lack of suitable habitats. The places of their occurrence in the vicinity of the Bohemian Forest lakes represent their epiarea only. For instance, the occurrence of *Orthetrum cancellatum* at Plešné Lake exceeds the altitudinal limit of the species in the Czech Republic. The locality of highest altitude known so far is 940 m a.s.l. (Nový Svět – Chalupská slat', 6947, DOLNÝ et al., 2007). Moreover, larvae require shallow habitats not yet overgrown with submerged aquatic vegetation.

#### Disputable species and entomofaunistics

The most disputable finding is that of *Aeshna viridis* collected by SENOO (2009) in an outlet of Černé Lake, which would represent a desirable new species to the fauna of the Czech Republic. *Ae. viridis* represents a Palaearctic, (West)Siberian species extending from north and eastern Europe (Belarus, Poland, western Ukraine), south to the Carpathians (Hungarian Plain) and northern Balkans, with scattered and isolated subareas in Denmark, the Netherlands, northern Germany and Austria, but completely missing in the Alps (SCHMIDT 1975, ASKEW 1988, 2004, HÄMÄLÄINEN 1983, GORB et al. 2000, DIJKSTRA & LEVINGTON 2006). In the Czech Republic, it can be expected especially in the Sudetes (cf. DOLNÝ et al. 2007), because the nearest locality to the territory of the Czech Republic (Węgliniec near Jelenia Góra in Poland) is situated about 30 km north of the border (cf. BORKOWSKI 1999, DOLNÝ et al. 2007). Its occurrence just in the Bohemian Forest lakes seems to be unlikely. This stenotopic species breeds in standing, acid to neutral moorland water bodies of the type often frequented by *Aeshna juncea* but only at low altitude (ASKEW 1988, 2004). Contrary to other species of *Aeshna* showing little preference for particular plants, females of *Ae. viridis* preferably oviposit in submerged leaves of *Stratiotes alboboides* (missing in the littoral of the lakes and banks of their inlets and outlets) although *Typha* and *Sparganium* may also sometimes be used (SCHIEMENZ 1953, NORLING 1971). The nearest localities to the Bohemian Forest are located near Vienna in Austria. However, it inhabits quite different habitats there being found mostly in backwaters of colline and lowland mid-sized rivers (RAAB et al. 2006). Historically, *Ae. viridis* have been recorded from the Czech Republic but the re-examination of the material in question shows it actually belongs to *Ae. cyanea* (cf. PERUTÍK 1957, JEZIORSKI 1998, DOLNÝ et al. 2007).

Findings of dragonflies in the Bohemian Forest lakes contribute to the mapping of the distribution of individual species within the Czech Republic. Since there are long-term extensive mapping programs of Odonata based on the widely used uniform grid system (ZELENÝ 1972, BUCHAR 1982, ZELENÝ & PULPÁN 1982, SOLDÁN 1980) that have cumulated more than 70 000 records (HANEL 1995a,b, HANEL & ZELENÝ 2000, DOLNÝ et al. 2007), we are able to add some new “quadrate records”. It concerns the quadrates 6845 (Laka, Černé, and Čertovo lakes), 6946 (Prášílské Lake), and 7249 (Plešné Lake). From the quadrate 6845, *Ae. subarctica* was recorded for the first time (otherwise known from the quadrates 6947, 7046, and

7149). In the quadrat 6946, there were no new species, since a detailed attention has been paid to this area (PERUTÍK 1957, HOLUŠA 1996, 2000) and at least 16 species have been collected here (ZELENÝ & HANEL 2000, ZELENÝ 2004a, DOLNÝ et al. 2007). Eight of them had been collected before 2000 in Černé and Laka lakes (6845). New “quadrat records” were acquired from the quadrat including Plešné Lake (7249) that have been relatively overlooked by odonatologist in the past – there are no data on the occurrence of dragonflies except for *Coenagrion hastulatum* and *Sympetrum flaveolum* (Linnaeus, 1758) (HANEL & ZELENÝ 2000, DOLNÝ et al. 2007). Five species (*Aeshna cyanea*, *Ae. subarctica*, *Libellula quadrimaculata*, *Somatochlora metallica*, *Sympetrum danae*) found in Plešné Lake are recorded from the quadrat 7249 for the first time. As far as we know, no data on the Odonata occurrence have been published from the German lakes yet. Consequently, all finding of dragonflies (altogether 15 species, Table 7) in German lakes represent new “quadrat records”.

Detailed and extensive knowledge of the distribution of dragonflies in the Czech Republic (HANEL & ZELENÝ 2000, DOLNÝ et al. 2007) enable to predict several species very likely occurring in the Bohemian Forest lakes. Given the distribution of dragonflies in the quadrates where the lakes are located in and high vagility of many species, there are at least seven species the occurrence of which seems to be likely in the lakes and their inlets and outlets. Beside *Cordulegaster bidentata* Sélys, 1843 and *Ae. affinis* Van der Linden, 1823 collected at the Prášily village (KREJČÍ 1892), these are *Somatochlora alpestris* (Sélys, 1840), *S. arctica* (Zetterstedt, 1840), *Anax imperator* Leach, 1815, and *Libellula depressa* Linnaeus, 1758, known from the quadrat 6845 (Laka, Černé, and Čertovo lakes) and 6946 (Prášilské Lake), and *Sympetrum flaveolum* (Linnaeus, 1758) from the quadrat 7249 (Plešné Lake). Especially *S. alpestris* could occur in the lakes, because the habitat fully corresponds to species requirements and it could escape our attention. Contrary to *S. arctica* that prefer very small peat bog water bodies (usually up to 1 m<sup>2</sup>) and are usually not accompanied by larvae of any other dragonflies, larvae of *S. alpestris* inhabit larger water bodies. They are often accompanied by *Aeshna juncea*, *Ae. subarctica*, *Enallagma cyathigerum*, and *Leucorrhinia dubia* (WILDERMUTH 1987, BROCKHAUS 1994, HOLUŠA 1995, 1997, ZELENÝ 2004a, PETR 2000, DIJKSTRA & LEVINGTON 2006, DOLNÝ et al. 2007), which inhabit our lakes. Both species of the genus *Somatochlora* have been collected in Štrbské Pleso Lake in the High Tatra Mts. (TRPIŠ 1965, STRAKA 1990).

Similar species, the occurrence of which cannot be excluded especially in the German lakes, is *Erythromma lindenii* (Sélys, 1840) of the family Coenagrionidae. This rather Mediterranean (or submediterranean, Westmediterranean according to DOLNÝ et al. 2007) species is widespread from the Iberian Peninsula and north Africa across southern Europe to Balkans (northern area limits in Romania, BULIMAR 1984), Turkey and Syria, with isolated subareas in Bavaria, Austria, Poland and north Germany (considered a separate subspecies, *E. lindenii lacustre* Beutler, 1985 in the latter case). Recently it occurs in at least 15 quadrates in Bavaria, some of them (6339, 6741, 6742) are situated in the Regen (Řezná) River basin close to the Czech border (ASKEW 1988, 2004, KUHN & BURBACH 1998, BERNARD 2000, BROCKHAUS & FISHER 2005, RAAB et al. 2006, DOLNÝ et al. 2007). Larvae prefer slow-flowing rivers and larger mesotrophic standing waters. They require habitats overgrown with rich vegetation and well oxygenated water.

#### Composition of taxocenoses and species abundance

There are no data on long-term changes in composition or abundance of dragonflies in the studied lakes. Judging from the comparison with the records published by KREJČÍ (1892) and HOLUŠA (2000), there are no pronounced changes in species composition within the past century. Acidification of aquatic habitats probably did not affect dragonflies as severely as

other aquatic biota. The most frequent and abundant species in the Bohemian Forest lakes belong to *Coenagrion hastulatum*-*Leucorrhinia dubia*-*Aeshna juncea* taxocenosis (according to the classification by HANEL & ZELENÝ 2000) inhabiting mires. It includes particularly acidotolerant species (often tyrphobiont and tyrphophilous species). The group of species occurring together with the three above mentioned species includes *Aeshna subarctica*, *Sympetrum danae*, *Enallagma cyathigerum*, *Cordulia aenea*, and *Libellula quadrimaculata*. Generally, species inhabiting (or specialised on) different mire habitats are obviously able to realise their life cycle at water pH of 4.0–5.0 as shown for at least 8 species, the larvae of which have been collected in these habitats (cf. PETR 2000, DOLNÝ et al. 2007). These very tolerant species are often supplemented by eurytopic species able to live from eutrophic to dystrophic waters (e.g., *Pyrrhosoma nymphula*, *Ischnura elegans*, *Aeshna cyanea*, *Somatochlora metallica*), which are the most frequent species in the lakes.

The only quantitative data by HOLUŠA (2000) indicated dragonflies to be relatively sparse at all the localities investigated. He found low densities of most species, except for the common species *Pyrrhosoma nymphula* in Prášilské and Laka lakes. According to our opinion, the most abundant species in the Bohemian Forest lakes is *Aeshna cyanea*, eurytopic species in the whole Czech Republic (DOLNÝ et al. 2007). Larvae inhabit not only lakes themselves but, contrary to most other species collected, also pools and temporary pools in the close vicinity of lakes. The species occurs in all the lakes investigated, showing apparently higher densities in German lakes, particularly in Rachelsee. Larvae prefer the littoral with both submerged and emerged vegetation, but frequently occur at places without vegetation, at stony bottom with sparse organic debris. In Rachelsee, we estimated their densities in October 2007: they reached 20–50 ind.m<sup>-2</sup> at places overgrown with plants but only up to 10–20 ind.m<sup>-2</sup> at places free of vegetation. In lakes with sparse occurrence of larvae (e.g., Čertovo Lake), they exhibited much lower densities (several specimens per square meter).



Fig. 13. Considerable differences in colour patterns of the larvae of *Aeshna cyanea* collected from different substrata (see text for details).

We have noticed considerable differences in colour patterns of the larvae apparent especially in large and ultimate size cohorts (probably 3-year-old larvae). Those collected in vegetation were generally lighter, dark yellowish to light brownish with well apparent light, pale yellowish to whitish spots on head, thorax and abdominal terga. On the contrary, larvae collected from stony substrata and compact rock were generally darker, brownish to pitch brown or blackish with less numerous diffused or even hardly distinguishable lighter colour patterns; numerous transitory types between these “extremes” can be observed (Fig. 13).

## Stoneflies (Plecoptera) – J. Bojková

### Species richness

Besides two species determined only at the generic level (*Perla* sp. and *Nemoura* sp.), altogether 13 species of 6 genera and 4 families have been found in the littoral zone of lakes (Tables 4, 8). Additional 19 species and 3 taxa determined to the generic level (*Isoperla* sp., *Amphinemura* sp., and *Protonemura* sp.) were recorded in lake inlets and outlets. The share of species of the Bohemian Forest lakes of the total species diversity of the Czech Republic can be estimated at 32%, although there is no up-to-date list of Plecoptera (RAUŠER 1977, MALENOVSKÝ et al. 2012). It represents more than 40% of species known from the Bohemian Forest (75 species; SOLDÁN 2004). Almost all species that inhabit small streams and springs in the Bohemian Forest also occur in the lakes. *Leuctra dalmoni* was recorded in the Bohemian Forest for the first time. Hardly any of the stonefly species found deserves a special faunistic attention with the exception of *Leuctra alpina*. It exhibits conjunctive area in the Alps in France, Switzerland, Germany, and Austria with a disjunction to the Bohemian Forest (PAPÁČEK & SOLDÁN 1995, GRAF et al. 2009).

The most valuable historical data on stoneflies were recorded by KŘELINOVÁ (1962). However, some of her determinations represented a misidentification due to an objective lack of knowledge at that times and the fact that some of species living here had not yet been described (for more details, see BOJKOVÁ 2009). First of all, this is the case of misidentified *Leuctra handlirschi* Kempny, 1898. This species actually lives in the Alps and does not occur either in the Bohemian Forest or the Czech Republic. This misidentification was followed by several authors dealing with Plecoptera of the lakes (SOLDÁN 1996, VRBA et al. 2003a, NEDBALOVÁ et al. 2006, SENOO 2009). The species living in the Bohemian Forest lakes and their inlets and outlets actually is *Leuctra pusilla*, which was described from the Carpathians (KRNO 1985), and has not been known from the Czech Republic till present (BOJKOVÁ 2009).

### Stoneflies of the lake littoral

On average six species were found in the lake littoral. The highest number of species was recorded in Prášilské Lake (11 species). Generally, fewer species were found in the German lakes (1–3 species) probably due to a short history of research of these lakes (no data available from the period before the impact of acidification) as well as their (peaty) littoral, less favourable for stoneflies. The majority of species were collected in imaginal stage by sweeping. Despite a low vagility of stoneflies, these imagines could reach the lake littoral from running water habitats nearby. Correct information on the diversity of lakes gives the data based on semiquantitative samples of larvae (E. Křelinová, M. Jezberová, T. Soldán, and L. Ungermanová leg.; Table 8). Only four species have been found in the larval stage in the littoral zone of lakes: *Nemoura avicularis*, *N. cinerea*, *Nemurella pictetii*, and *Leuctra nigra*. Eurytopic *N. cinerea* and *N. pictetii* were common and abundant inhabitants of the lakes; they were found repeatedly in all of them. They are the only stonefly species widely

occurring in standing waters across their whole area (both species are Euro-Siberian). Unlike *N. cinerea*, *N. pictetii* is not a ubiquitous species, because it is not resistant to pollution. Larvae of *L. nigra* were found in three lakes (Černé, Čertovo, Prášilské). Mass occurrence was observed along inlets flowing through sedge belt of the littoral of Laka Lake and Kleiner Arbersee, but no larvae were collected in the lakes themselves. It was also common in inlets of other lakes. *L. nigra* has rarely been found in standing waters. Its larvae prefer springs and small streams and dwell in sandy deposits and coarse organic matter (BOJKOVÁ & HELEŠIČ 2009, GRAF et al. 2009). In the studied lakes, *L. nigra* was collected only in coarse woody debris near inlets. These three species are resistant to acidity and often predominate in very acid waters (BRAUKMANN 2001, THOMSEN & FRIBERG 2002, TIXIER & GUÉROLD 2005). Predominance could be related to a release of competitive interactions or predation pressure in acidic habitats from those species intolerant to low pH (BRAUKMANN 2001). These species are, however, negatively affected by acid conditions due to low food quality (GROOM & HILDREW 1989, THOMSEN & FRIBERG 2002). The fourth species found in the larval stage is *N. avicularis*, which inhabit Černé and Čertovo lakes. It is a common inhabitant of lacustrine habitats in Scandinavia and Great Britain (e.g., BRITAIN 1973, LILLEHAMMER 1985). It prefers oligotrophic lakes from lowlands to montane zones (BRODERSEN et al. 1998, ZWICK 2004), but it was not recorded from alpine lakes in the Alps and the Tatra Mts. (cf. FÜREDER et al. 2006, KRNO et al. 2006). Similarly to the above mentioned species, it is acid resistant (BRAUKMANN & BISS 2004, TIXIER & GUÉROLD 2005).

The remaining species referred as lake inhabitants by KŘELINOVÁ (1962) were collected only in the imaginal stage. Moreover, they were often collected singly and mostly females occurred. Since females can fly more intensively than males, incidental occurrence on the lake shore cannot be excluded. These species can be expected to develop in the mouths of inlets and littoral zone in the immediate vicinity, e.g., *Leuctra* spp. (*L. aurita*, *L. autumnalis*, *L. digitata*, *L. fusca*, *L. inermis*, *L. pusilla*), *Protonemura* spp. (*P. auberti*, *P. hrabei*, *P. montana*), and *Nemoura marginata*. Indeed, larvae of *L. pusilla*, *L. inermis*, and *P. auberti* were collected in inlets close to the lake littoral.

On the other hand, a female of *Capnia vidua* found in Černé Lake in the vicinity of an inlet can be expected to dwell in the lake itself, as it was found in many mountain lakes (19 of 45 lakes investigated) in the Tatra Mts. (KRNO et al. 2006). Imagines of *C. vidua* were found in inlets of five lakes, but larvae were found neither in inlets nor in lakes. However, this species emerges in early spring and can be overlooked by late sampling. Also *Leuctra digitata* was not found in larval stage although its imagines occur relatively numerously in the lake littoral. Both males and females were collected on sedges next to an outlet of Laka Lake and in a waterlogged shore of Prášilské Lake, where the main inlet enters the lake. Also KŘELINOVÁ (1962) collected imagines along the shore of Prášilské Lake and labelled the material by this lake. In our opinion, larvae of this species most likely develop in shallow vegetated littoral near inlets and outlets, albeit in low numbers, so that they are not detectable by sampling with a net. BOJKOVÁ (unpubl.) observed a similar case in the Krušné Hory Mts. (Erzgebirge/Ore Mts.), where larvae dwelled in silty littoral with water seepages of acidic oligotrophic mountain pond Lieche (Rolavský Rybník). *L. digitata* was found in high numbers also in acidic, peaty outflows of moorland and fens overgrown by sedges (Krušné Hory Mts. and Beskydy Mts.; BOJKOVÁ, unpubl.). Imagines of *Leuctra pusilla* and *Protonemura auberti* were repeatedly collected in the lake littoral. Both species prefer small streams with a significant share of coarse particulate organic matter, and stony-gravel (*L. pusilla*) or gravel-sandy substrate (*P. auberti*). Their larvae can be expected to survive in low numbers in the mouths of inlets with these substrates.

**Table 8.** Species/taxa of stoneflies (Plecoptera) found in the Bohemian Forest lakes in 1892–2010. Species collected in the lakes (see Table 1 for their codes) are in bold; occurrence in individual habitats is distinguished to findings in a lake (L), its inlets (I) and outlet (O); references to unpublished records are not in small caps, i.e., refer to the collector(s) and the year of finding(s).

Family /Species	CN	CT	PL	PR	LA	GA	KA	RA	References
<b>Perlidae</b>									
<i>Perla</i> sp.		L?							FRÍČ & VÁVRA 1897
<b>Perlodidae</b>									
<i>Diura bicaudata</i> (Linnaeus, 1758)		O		I	I,O	I	I,O		Jezberová 2002; Soldán 2002
<i>Isoperla</i> sp.	O			I	I,O	I	I		Bojková 2009, 2010
				O	O				Chvojka 1991
<b>Chloroperlidae</b>									
<i>Chloroperla tripunctata</i> (Scopoli, 1763)		O							KLAPÁLEK 1903
<i>Siphonoperla torrentium</i> (Pictet, 1841)				O	O				Chvojka 1991
				O		I,O	I,O		Bojková 2010
<b>Taeniopterygidae</b>									
<i>Brachyptera seticornis</i> (Klapálek, 1902)						I			KLAPÁLEK 1903
						O			Soldán 2002
				I		I	I,O		Bojková 2010
<b>Nemouridae</b>									
<i>Amphinemura standfussi</i> (Ris, 1902)				I					Chvojka 2007
		O			I			O	Bojková 2009
<i>Amphinemura sulcicollis</i> (Stephens, 1836)		I,O			I				Jezberová 2002
		O			O	I,O	I,O		Bojková 2010
<i>Amphinemura</i> sp.	O		O		I,O				Soldán 1985, 1986, 1995
<i>Nemoura avicularis</i> Morton, 1894	I,L								KŘELINOVÁ 1962
	L	L							UNGERMANOVÁ 2009
	I,L	I,L				I			Bojková 2010
<i>Nemoura cambrica</i> Stephens, 1835	I								Soldán 2002
<i>Nemoura cinerea</i> (Retzius, 1783)		O				L			KLAPÁLEK 1903
	I,L,O	L,O		I,L					KŘELINOVÁ 1962
	I,L,O	I,L,O	I,L,O	I,L,O	I,L,O	I,L,O	I,L,O	I,L,O	Soldán 1985, 1986, 1989, 1990, 1995
	L				L				Chvojka 1991
	I,L	I,L,O	I,L,O	I,O		O			Jezberová 2002; Soldán 2002
	L	L			O				Chvojka 2007
	L	L	L	L	L				UNGERMANOVÁ 2009
	I,L	I,L,O	I,L,O	I,L,O	I,L,O	I,L,O	L,O	I,L,O	Bojková 2010

Table 8. Continued

Family / Species	CN	CT	PL	PR	LA	GA	KA	RA	References
<i>Nemoura marginata</i> Pictet, 1835			O	L					KŘELINOVÁ 1962 SOLDÁN 1996
<i>Nemoura</i> sp.	L							I	FRIČ & VÁVRA 1897 Bojková 2010
<i>Nemurella pictetii</i> (Klapálek, 1900)		O							KLAPÁLEK 1903
	L,I	O		L					KŘELINOVÁ 1962
	L		L	L	L				Soldán 1985, 1986, 1989, 1990, 1995
					I				Chvojka 1991
							I	I	SCHAUMBURG 2000
	I,L	I,L	I,L,O	I	I	L	I	I	Jezberová 2002; Soldán 2002
	L						I		Chvojka 2007
<i>Protonemura auberti</i> Illies, 1954	I,L,O	I	I,L,O	I,L	I,L		I	I,L	Bojková 2009, 2010
	I	L	L						KŘELINOVÁ 1962
	L	L	L	L					Soldán 1985, 1986, 1989, 1990, 1995,
					I				Chvojka 1991
	I	I,O		I	I,L,O	O	O		Jezberová 2002; Soldán 2002
	L			I	I	I	I		Chvojka 2007
	I	I,O		I,L,O	I,O	I	I	I,O	Bojková 2009, 2010
<i>Protonemura</i> cf. <i>lateralis</i> (Pictet, 1836)					I				Bojková 2010
<i>Protonemura hrabei</i> Rausser, 1956				L					KŘELINOVÁ 1962
<i>Protonemura intricata</i> (Ris, 1902)	I							I	Chvojka 2007
									KŘELINOVÁ 1962
					O				Chvojka 1991
<i>Protonemura meyeri</i> (Pictet, 1941)		O			I		O		Bojková 2010
<i>Protonemura montana</i> Kimmins, 1941				L					KŘELINOVÁ 1962
<i>Protonemura</i> sp.			I				I	I	Bojková 2010
<b>Capniidae</b>									SCHAUMBURG 2000
<i>Capnia vidua</i> Klapálek, 1904									Jezberová 2002
	I,L?				I				Chvojka 2007
	I	I			I	I	I		Bojková 2010
<b>Leuctridae</b>									
<i>Leuctra alpina</i> Kühnreiter, 1934					I				Chvojka 2007
			I						Bojková 2010

Table 8. Continued

Family / Species	CN	CT	PL	PR	LA	GA	KA	RA	References
<i>Leuctra aurita</i> Navás, 1919				L					KŘELINOVÁ 1962
				L				I	Chvojka 2007
<i>Leuctra autumnalis</i> Aubert, 1948					I				Bojková 2010
				L					KŘELINOVÁ 1962
			O		I				Jezberová 2002
					I				Chvojka 2007
<i>Leuctra braueri</i> Kempny, 1898					I				Bojková 2010
		O							KLAPÁLEK 1903
<i>Leuctra dalmonii</i> Vinçon et Murányi, 2006					O			O	Bojková 2008, 2009
<i>Leuctra digitata</i> Kempny, 1899							I		Bojková 2010
				L					KŘELINOVÁ 1962
			L	L	L				Soldán 1985, 1986, 1989, 1990, 1995
			I		O				Jezberová 2002
				O	L,O				Chvojka 2007
<i>Leuctra fusca</i> (Linnaeus, 1758)			I	L,O	I,L,O				Bojková 2008, 2010
	I			L					KŘELINOVÁ 1962
									KŘELINOVÁ 1962
					O				KLAPÁLEK 1903
<i>Leuctra hippopus</i> Kempny, 1899	I								KŘELINOVÁ 1962
					O				Chvojka 1991
					O				Bojková 2010
									KLAPÁLEK 1903
<i>Leuctra nigra</i> (Olivier, 1811)					L				KŘELINOVÁ 1962
	I	O							KLAPÁLEK 1903
	L	L	L	L	L				Křelinová 1962
		L,O	L	L	L				Soldán 1985, 1986, 1989, 1990, 1995
	I,O	I,L,O	I	O	I	I	I	I	Chvojka 1991
	I				I,O				Jezberová 2002
									Chvojka 2007
<i>Leuctra pseudocingulata</i> Mendl, 1968	I,L,O	L							UNGERMANOVÁ 2009
	I	I,L,O	I,L,O	I	I,O	I	I,O	I	Bojková 2009, 2010
	I	I	I	I	I	I	I		Jezberová 2002
<i>Leuctra pseudosignifera</i> Aubert, 1954	I	I	I	I	I				Chvojka 2007
	I,O	O		I	I			O	Bojková 2009, 2010
	I								Chvojka 2007

Table 8. Continued

Family / Species	CN	CT	PL	PR	LA	GA	KA	RA	References
<i>Leuctra pusilla</i> Krno, 1985	I		L	L					KŘEJLINOVÁ 1962
	L		L						Soldán 1985, 1986, 1989, 1990, 1995
	I			O					Chvojka 1991
	I								Jezberová 2002; Soldán 2002
	I								Chvojka 2007
<i>Leuctra rauscheri</i> Aubert, 1957	I				I,L,O	I	I	I	Bojková 2009, 2010
	I								KŘEJLINOVÁ 1962
					O				Soldán 1989, 1990
					O				Chvojka 1991
	I					I		Bojková 2010	
<b>Total number of species</b>	<b>17</b>	<b>14</b>	<b>11</b>	<b>17</b>	<b>23</b>	<b>13</b>	<b>14</b>	<b>12</b>	
Number of species in lakes	7	6	6	12	6	2	1	2	
Number of species in outlets	6	11	6	4	14	5	8	5	
Number of species in inlets	14	8	6	8	17	13	13	9	
Number of species in inlets and outlets	16	13	9	10	23	13	14	12	

## Impact of acidification

The comparison of Plecoptera taxocenoses of lakes before and after the acidification is possible especially owing to KŘELINOVÁ (1962) who collected material in some of the Czech lakes in the 1950s and 1960s. Although lake stoneflies, as well as mayflies and caddisflies, have been studied as a part of extensive research of aquatic insects of the Czechoslovakia, the data collected are rather fragmentary or not fully compatible when analysing long-term changes. There is no historical information on stoneflies of the German lakes and some Czech lakes were studied only occasionally in the pre-acidification period. Changes in species richness and composition of Plecoptera taxocenoses over the past 110 years are possible to evaluate regarding Černé and Čertovo lakes. A reliable comparison of the 1950s and recent data is possible to make for Prášílské and Černé lakes, and plausibly also for inlets of Černé Lake, while the material from other Czech lakes collected in the 1950s is incomplete. In spite of these rather fragmentary data, several trends are obvious.

At the end of the 19<sup>th</sup> century, FRIČ & VÁVRA (1897) found the only acid sensitive stonefly, *Perla* sp., in Čertovo Lake. Species of this genus never occur in acidified waters (BRAUKMANN 2001, TIXIER & GUÉROLD 2005). For instance, a considerable decline of a montane stonefly *Perla grandis* Rambur, 1842 has been observed in acidified streams in Bohemia (BOJKOVÁ & KROČA 2011). This species completely disappeared from historical localities in the Krkonoše (Giant) Mts., which were strongly affected by acidification in the second half of the last century. KLAPÁLEK (1903) found *Chloroperla tripunctata* in the outlet of Čertovo Lake at the beginning of the 20<sup>th</sup> century. This species is considered relatively acid sensitive showing a strong preference for the higher pH streams within the range of pH 4.2–6.9 in Wales and Scotland (WEATHERLEY et al. 1993). The species was also found to re-colonise acidified streams after decreasing emissions of acidifying pollutants and increasing pH in lakes and streams in the English Lake District (TIPPING et al. 2002). Both stoneflies unlikely inhabit lacustrine habitats, but strong acidification of Čertovo Lake undoubtedly caused their vanishing from lake inlets and outlet. This indicates, in spite of fragmentary information on the reference state of habitats and taxocenoses that the diversity of lakes and surrounding aquatic habitats could change considerably. Acid resistant species, *Nemoura avicularis*, *N. cinerea*, and *Nemurella pictetii* found by KŘELINOVÁ (1962) in the 1950s, were most likely present much earlier but not distinguished to the species level. FRIČ & VÁVRA (1897) mentioned the larvae of *Nemoura* sp. These species were re-collected in the 1990s and 2000s, while their populations were probably reduced at the time of strong acidification of lakes. They were not repeatedly found in all lakes and were collected in much lower abundance in the late 1980s and the 1990s (SOLDÁN, unpubl. data).

The decline in species richness and probably also abundance of some species can be documented by the example of Prášílské Lake. Altogether 12 species were collected there in the 1950s (KŘELINOVÁ 1962, Table 8), though definitely not all of them lived in the lake itself and some species reached the lake littoral from its inlet as mentioned above. The lake and its inlet were repeatedly investigated after 1990 and only six species were found: *Nemoura cinerea*, *Nemurella pictetii*, *Protonemura auberti*, *Leuctra aurita*, *L. digitata*, and *L. nigra*. Moreover, *L. aurita* was collected as a single female, while a relatively rich population was observed in the 1950s (tens of specimens present in the Křelinová's collection). Stoneflies as a group are generally considered acid tolerant (RADDUM 1980, RADDUM et al. 1988, ØKLAND & ØKLAND 1986, BRAUKMANN 2001). However, individual species differ in their sensitivity to the impacts of acidity on the smaller scale than other invertebrates; although the scaling and definition of tolerance is not easy and globally valid (TIXIER & GUÉROLD 2005, BRAUKMANN 2001, RADDUM & SKJELKVÅLE 1995, HÄMÄLÄINEN & HUTTUNEN 1996). Beside several

species tolerant or indifferent to acidity and two genera of truly sensitive stoneflies (*Perla* and *Dinocras*), there are many species “slightly acid tolerant” and “relatively acid sensitive”. Twelve species found in Prášílské Lake include the examples of several species of different sensitivity and/or tolerance. *N. cinerea*, *N. pictetii*, and *L. nigra* represents the most acid resistant (or indifferent) stoneflies. HORECKÝ et al. (2002, 2006) observed their larvae to survive in the habitats with pH about 3.9–4.4 at several localities in the Brdy Mts. in the Czech Republic. *Protonemura auberti*, *Diura bicaudata*, and *Brachyptera seticornis* are common inhabitants of oligotrophic montane and submontane headwaters, which are acid tolerant due to naturally lower and/or seasonally variable pH of these habitats. The last resistant species found before and after the period of strong acidification is *Leuctra digitata*, which is an example of eurytopic species able to live in wide range of water quality. Its larvae can survive considerable salinity of 4.2‰ (MÜLLER & MENDEL 1979) and can occur in temporary acidic outflows of moorland and fens (BOJKOVÁ, unpubl.). Species considered slightly acid tolerant were not found recently at all (e.g., *Protonemura montana*, *P. hrabei*, *Leuctra fusca*) or were found in a single specimen (*L. aurita*) in Prášílské Lake. These species still occur in circum-neutral running waters in the Bohemian Forest close to areas affected by acidification.

Such a local decline in tolerant species can be observed in the inlets of Černé Lake. Common species of oligotrophic montane headwaters that were naturally tolerant (e.g., *Leuctra pusilla*, *L. rauscheri*, and *P. auberti*) survived. However, other species also expected to be relatively tolerant (e.g., *Leuctra hippopus* and *Protonemura intricata*) disappeared. These inlets are rather marginal habitats where these species might not survive impacts, which could be tolerated in their optimal habitats.

#### **Aquatic and semiaquatic bugs (Heteroptera) – M. Papáček**

The first records on water bug fauna of the Bohemian Forest glacial lakes have been published already more than 160 years ago (Table 9). They include mostly records on a single or a few species, namely *Glaenocoris propinqua*, *Notonecta glauca*, *Aquarius paludum*, and *Velia caprai*, yet referred under different names (cf. FIEBER 1848, FRIČ & VÁVRA 1897). Despite of a relatively long history of research, earlier literature data on other species remained very limited. More comprehensive data on the water bug fauna became available as late as after 2000. The data from the period 2000–2009, similarly as earlier data, are based mostly only on the samples collected in the littoral zone of the lakes.

#### **Species richness**

Altogether 34 species of water bugs have been found in the Bohemian Forest lakes (Table 9): 23 species of true water bugs (= aquatic bugs; Nepomorpha) belonging to 11 genera and 5 families, and 11 species of semiaquatic bugs (Gerromorpha) belonging to 7 genera and 4 families. The nepomorphan species found in the lakes represent about 88% of the Nepomorpha fauna of the Bohemian Forest and about 49% of fauna the whole Czech Republic, calculated from the complete list of true water bugs of the Czech Republic fauna, which also includes unconfirmed data. When excluding the unconfirmed data, 23 true water bug species match about 53% of the Czech Republic Nepomorpha. Eleven gerromorphan species found in the lakes represent about 58% of gerromorphan fauna of the Bohemian Forest and its foothills, as well as the whole Czech Republic Gerromorpha, including only species with well documented occurrence (see PAPÁČEK & SOLDÁN 1995, 2003; SOLDÁN et al. 1996).

A list of species found in more than two lakes is presented in Table 10. Seventeen water bug species, i.e. 50% of the whole water bug fauna of the lakes (13 species, i.e. 52% of aquatic and 4 species, i.e. 36% of semiaquatic species) inhabited three or more lakes. Twelve species (36%) were recorded commonly in 5–8 lakes.

**Table 9.** Species/taxa of aquatic and semiaquatic bugs (Heteroptera) found in the Bohemian Forest lakes in 1848–2011. Species collected in the lakes (see Table 1 for their codes) are in bold; occurrence in individual habitats is distinguished to findings in a lake (L), its inlets (I) and outlet (O); references to unpublished records are not in small caps, i.e., refer to the collector(s) and the year of finding(s).

Family / Species	CN	CT	PL	PR	L/A	GA	KA	RA	References
Infrasuborder <b>Nepomorpha</b>									
<b>Nepidae</b>									
<i>Nepa cinerea</i> Linnaeus, 1758					L				Papáček 1999
<b>Corixidae</b>									
<i>Cymatia bonsdorffii</i> (C.R. Sahlberg, 1819)					L				Papáček 1998, 1999
					L				Kment & Papáček 1999 (KMENT & SMĚKAL 2002)
					L	L			UNGERMANOVÁ 2009
					L				Papáček 2010, 2011
	L								FRIBER 1848 <sup>1)</sup>
<i>Glaenocoris propinqua</i> (Fieber, 1860)	L								Vávra 1896 (coll. Nat. Mus. Prague; KMENT, pers. comm.)
	L	L							FRÍČ & VÁVRA 1897 <sup>2)</sup>
	L <sup>3)</sup>	L <sup>3)</sup>	L <sup>3)</sup>	L <sup>3)</sup>	L <sup>3)</sup>	L <sup>3)</sup>	L <sup>3)</sup>	L <sup>3)</sup>	<sup>3)</sup> DUDA 1884, 1886, 1891, 1892; VEYDOVSKÝ 1891 <sup>4)</sup> ; HÜBER 1905; HOLDHAUS 1912; TEYROVSKÝ 1931; GULDE 1935 (reviewed by ROUBAL 1957)
			L						Štolc, date unknown, 1 male (neotype), 1 female (coll. Nat. Mus. Prague; KMENT, pers. comm.) (ROUBAL 1957; JANSSON 1986 <sup>5)</sup> )
	L		L	L					PAPÁČEK & SOLDÁN 1995; Papáček 1992, 1996, 1998, 1999
				L					KUBEČKA et al. 2000
			L	L					Papáček 2001, 2002
						L			Papáček 2007
					L				SYCHRA et al. 2008
			O	O					SENOO 2009
	L			L	L				UNGERMANOVÁ 2009
	L	L	L	L					TEXLOVÁ 2010
	L	L	L	L	L			L	Papáček 2010, 2011
	L	L	L	L					Sychra 2010

Table 9. Continued

Family / Species	CN	CT	PL	PR	LA	GA	KA	RA	References
<i>Callicorixa praeusta praeusta</i> (Fieber, 1848)			L	L	L				Papáček 1998, 1999
				L	L				Kiment & Papáček 1999
			L	L	L				Papáček 2001, 2002
			L	L					UNGERMANOVÁ 2009
	L								TEXLOVÁ 2010
<i>Corixa dentipes</i> Thomson, 1869	L	L	L	L	L				Sychra 2010
			L	L	L				Papáček 2010, 2011
<i>Corixa punctata</i> (Illiger, 1807)			L	L	L				Papáček 1999
					L				Papáček 2011
<i>Hesperocorixa sahlbergi</i> (Fieber, 1848)			L	L	L				Papáček 1998, 1999
				L	L				Kiment & Papáček 1999
				L	L				Papáček 2001
	L								Jezberová 2002
				L					TEXLOVÁ 2010
<i>Paracorixa concinna concinna</i> (Fieber, 1848)		L							Sychra 2010
	L	L			L				Papáček 2011
					L				Papáček 1998
	L								TEXLOVÁ 2010
			L	L					Papáček 2011
<i>Sigara (Pseudovermicorixa) nigrolineata nigrolineata</i> (Fieber, 1848)								L	SCHÖLL 1989
		L,O			L				Papáček 1992, 1998, 1999
			O						Jezberová 2002
	L	L	L	L	L	L			SENOO 2009
	L	L	L	L	L	L	L	L	UNGERMANOVÁ 2009
<i>Sigara (Retrocorixa) limitata limitata</i> (Fieber, 1848)	L	L	L	L	L	L	L	L	Papáček 2007–2011
	L	L	L	L	L	L	L	L	TEXLOVÁ 2010
	L	L	L,O					L	Sychra 2010
				L	L				UNGERMANOVÁ 2009
				L	L	L	L	L	UNGERMANOVÁ 2009
<i>Sigara (Retrocorixa) semistriata</i> (Fieber, 1848)						L			TEXLOVÁ 2010
			L		L		L	L	Sychra 2010
			L	L	L		L	L	Papáček 2011
			L	L	L				
			L	L	L				

Table 9. Continued

Family / Species	CN	CT	PL	PR	LA	GA	KA	RA	References
<i>Sigara (Subsigara) distincta</i> (Fieber, 1848)	L	L	L	L	L	L	L	L	UNGERMANOVÁ 2009
	L	L	L	L	L	L	L	L	TEXLOVÁ 2010
	L	L	L	L	L	L	L	L	Sychra 2010
	L	L	L	L	L	L	L	L	Papáček 2010, 2011
<i>Sigara (Subsigara) falleni</i> (Fieber, 1848)	L	L	L	L	L	L	L	L	UNGERMANOVÁ 2009
	L	L	L	L	L	L	L	L	TEXLOVÁ 2010
	L	L	L	L	L	L	L	L	Sychra 2010
	L	L	L	L	L	L	L	L	Papáček 2010, 2011
<i>Sigara (Subsigara) fossarum</i> (Leach, 1817)	L	L	L	L	L	L	L	L	UNGERMANOVÁ 2009
	L	L	L	L	L	L	L	L	TEXLOVÁ 2010
	L	L	L	L	L	L	L	L	Sychra 2010
	L	L	L	L	L	L	L	L	Papáček 2010, 2011
<i>Sigara (Vermicorixa) lateralis</i> (Leach, 1817)	L	L	L	L	L	L	L	L	Papáček 1998, 1999
	L	L	L	L	L	L	L	L	Kment & Papáček 1999
	L	L	L	L	L	L	L	L	Papáček 2002
	L	L	L	L	L	L	L	L	UNGERMANOVÁ 2009
<b>Micronectidae</b>	L	L	L	L	L	L	L	L	TEXLOVÁ 2010
	L	L	L	L	L	L	L	L	TEXLOVÁ 2010 <sup>6)</sup>
	L	L	L	L	L	L	L	L	Papáček 2011
	L	L	L	L	L	L	L	L	Papáček 2011
<b>Nautoridae</b>	L	L	L	L	L	L	L	L	Papáček 2011
	L	L	L	L	L	L	L	L	Papáček 2011
	L	L	L	L	L	L	L	L	Papáček 2011
	L	L	L	L	L	L	L	L	Papáček 2011
<b>Notonectidae</b>	L	L	L	L	L	L	L	L	FRÍČ & VÁVRA 1897
	L	L	L	L	L	L	L	L	Papáček 1992, 1998, 1999
	L	L	L	L	L	L	L	L	Kment & Papáček 1999
	L	L	L	L	L	L	L	L	SENOC 2009
<i>Notonecta (Notonecta) glauca</i> Linnaeus, 1758	L	L	L	L	L	L	L	L	UNGERMANOVÁ 2009
	L	L	L	L	L	L	L	L	TEXLOVÁ 2010
	L	L	L	L	L	L	L	L	Sychra 2010
	L	L	L	L	L	L	L	L	Papáček 2007–2011
<i>Notonecta lutea</i> Müller, 1776	L	L	L	L	L	L	L	L	Papáček 1998
	L	L	L	L	L	L	L	L	Papáček 2007, 2008
	L	L	L	L	L	L	L	L	TEXLOVÁ 2010
	L	L	L	L	L	L	L	L	TEXLOVÁ 2010

Table 9. Continued

Family / Species	CN	CT	PL	PR	LA	GA	KA	RA	References
<i>Notonecta maculata</i> Fabricius, 1794							L		Papáček 2007
<i>Notonecta reuteri reuteri</i> Hungerford, 1928	L								TEXLOVÁ 2010
<i>Notonecta viridis</i> Delcourt, 1909	L								TEXLOVÁ 2010
<b>Pleidae</b>									
<i>Plea minutissima minutissima</i> Leach, 1817			L						UNGERMANOVÁ 2009
Infrasuborder <b>Gerromorpha</b>			L	L					Papáček 2011
<b>Hebridae</b>									
<i>Hebrus (Hebrusella) ruficeps</i> Thomson, 1871				L	L				Sychra 2010
<b>Hydrometridae</b>									
<i>Hydrometra gracilenta</i> Horváth, 1889			L						Sychra 2010
<b>Veliidae</b>									
<i>Microvelia (Microvelia) reticulata</i> (Burmeister, 1835)				L					Papáček 1998, 1999
				L					Kiment & Papáček 1999
			L	L	L				Papáček 2010
			L	L	L				Sychra 2010
<i>Velia (Plestiovelia) caprai caprai</i> Tamanini, 1947	L		O						FRIČ & VÁVRA 1897 <sup>b)</sup>
			O						Jezberová 2002
			O						SENOC 2009
					L			L	TEXLOVÁ 2010
	I	I	O	I,O	I		I	I	Papáček 2007, 2008
	O	O	O	O	O				Sychra 2010
<b>Gerridae</b>									
<i>Aquarius paludum paludum</i> (Fabricius, 1794)	L								FRIČ & VÁVRA 1897 <sup>b)</sup>
				L					Papáček 1999
							L		Sychra 2010
			L						TEXLOVÁ 2010 <sup>9)</sup>
<i>Gerris (Gerris) argentatus</i> Schummel, 1832			L						UNGERMANOVÁ 2009
<i>Gerris (Gerris) gibbifer</i> Schummel, 1832			L						Sychra 2010
<i>Gerris (Gerris) lacustris</i> (Linnaeus, 1758)				L	L				SYCHRA et al. 2008
			L						UNGERMANOVÁ 2009
			L	L	L			L	TEXLOVÁ 2010
	L	L,O	L,O	L,O	L		L	L	Sychra 2010

Table 9. Continued

Family / Species	CN	CT	PL	PR	LA	GA	KA	RA	References
<i>Gerris (Gerriselloides) lateralis</i> Schummel, 1832			L						Sychra 2010
<i>Gerris (Gerris) odontogaster</i> (Zetterstedt, 1828)			L	L					Papáček 1998, 1999
			L						UNGERMANOVÁ 2009
			L	L		L		L	TEXLOVÁ 2010
	L		L	L		L			Sychra 2010
<i>Limnoporus rufoscutellatus</i> (Latreille, 1807)			L						TEXLOVÁ 2010
<b>Total number of species</b> , Nepomorpha+Gerromorpha	<b>14+3</b>	<b>8+2</b>	<b>13+9</b>	<b>13+3</b>	<b>18+4</b>	<b>7+3</b>	<b>7+4</b>	<b>6+3</b>	
Nepomorpha+Gerromorpha in lakes	14+3	8+1	13+8	13+2	18+4	7+3	7+3	6+3	
Nepomorpha+Gerromorpha in inlets and outlets	0+1	2+1	2+2	2+1	0+2	0+0	0+1	0+1	

<sup>1)</sup> Most probably the earliest reference on *G. propinqua* from the Bohemian Forest; a specimen was collected by Dr. Kolenati and referred as *Corisa carinata* Sahlb. (see JANSSON 1986: p. 26 for synonymy).

<sup>2)</sup> Referred as *Glaenocorisca cavifrons* Thomson, 1869; *Glaenocorisca propinqua* (Fieber, 1860) and *Glaenocorisca cavifrons* (Thomson, 1869), downgraded by OSSIANILSSON (1960) to the subspecies of *G. propinqua* and later again upgraded by JANSSON (2000) to the species level, are very similar species with variable specimens (e.g., BROWN 1946). These species differ only by some minute characters of male pala and parameres. Probably, this is a reason of some mistakes and confusions in published data. Only *Glaenocorisca propinqua* is distributed in central Europe (JANSSON 1986, 1995) and inhabits the Bohemian Forest lakes.

<sup>3)</sup> Locality referred as “Šumava” (= Bohemian Forest) or “Šumavská jezera” (= Bohemian Forest lakes).

<sup>4)</sup> Referred as *Corisa “flavifrons”*.

<sup>5)</sup> Referred as *Glaenocorisca propinqua* (Fieb.) (*cavifrons* Thomson) (see ROUBAL 1957); JANSSON (1986) designated a male specimen from the sample collected by Štolc in PL as the neotype.

<sup>6)</sup> One female specimen, partly macerated; *Micronecta (Dichaetonecta)* cf. *scholtzi* (Fieber, 1860).

<sup>7)</sup> Probably *Aquatius paludum*; referred as *Hydrometra paludum* Fabricius, 1794.

<sup>8)</sup> Probably *Velia caprai*; referred as *Velia currrens*. According to ANDERSEN (1995): “Most records of ‘*Velia currrens*’ earlier than TAMANINI (1947), refer to other species of *Velia*.” *Velia (Plesiovelia) currrens* (Fabricius, 1794) is not distributed in the Czech Republic (e.g., ANDERSEN 1995).

<sup>9)</sup> This finding (partly destroyed female specimen) was originally misidentified as *Aquatius najas*.

**Table 10.** Most frequently distributed species of aquatic and semiaquatic bugs (Heteroptera) in the Bohemian Forest lakes (recent state in 2011; a number of lakes, where the species was recorded till 1999, is given in parentheses).

Number of lakes	Nepomorpha	Gerromorpha
8	<i>Sigara nigrolineata</i> (2)	–
7	<i>Glaenocorisa propinqua</i> (4) <i>Sigara distincta</i> (0) <i>Sigara fossarum</i> (0) <i>Notonecta glauca</i> (4)	–
6	<i>Sigara lateralis</i> (3) <i>Sigara semistriata</i> (0)	–
5	<i>Callicorixa praeusta</i> (3) <i>Hesperocorixa sahlbergi</i> (3) <i>Sigara falleni</i> (0)	<i>Gerris lacustris</i> (0) <i>Gerris odontogaster</i> (2)
4	<i>Paracorixa concinna</i> (1)	<i>Aquarius paludum</i> (2)
3	<i>Corixa dentipes</i> (0)	<i>Microvelia reticulata</i> (1)

*Glaenocorisa propinqua* and *Sigara distincta* are highly acid-tolerant inhabitants of deep open and cold meso- to oligotrophic lentic habitats. *S. fossarum* occurs especially in oligotrophic and dystrophic habitats including acidified waters.

*Callicorixa praeusta*, *Hesperocorixa sahlbergi* (species preferring forest shaded ponds with rich vegetation), *Paracorixa concinna*, *Sigara falleni*, *S. lateralis* (species preferring shallow water bodies without vegetation), *S. nigrolineata*, *S. semistriata*, and *Notonecta glauca* represent (relatively) eurytopic acido-tolerant species, which inhabit also waters at higher altitudes in mountains. All these species are good to outstanding migrants. Most of them prefer water bodies with the bottom covered by organic matter or sand.

*Gerris lacustris* and *G. odontogaster*, recorded from five lakes, are relatively common and widely distributed semiaquatic bugs. *G. lacustris* inhabits both lentic (especially) and lotic habitats with littoral vegetation that are sheltered from adjacent landscape by forest or trees. *G. odontogaster* is known only from lentic habitats, often accompanying *G. lacustris*. Populations of these species were extremely low in lakes that are poor in littoral vegetation.

Aquatic bug *Corixa dentipes* and semiaquatic bug *Microvelia reticulata* were found in three lakes. *C. dentipes* is a relatively stenotopic species preferring lentic water bodies with rich littoral vegetation. This species is known also from peaty habitats. *M. reticulata* prefers the littoral overgrown with rich vegetation, which occurs especially in Laka, Plešné, and Prášilské lakes, where both species were found syntopic.

Habitat characteristics of species presented in Table 10 generally follow the review by KMENT (2001) and data by WRÓBLEWSKI (1980), SAVAGE (1989), PAPÁČEK (1991), WOLLMANN (2000), and KMENT & SMÉKAL (2002). More detailed characteristics of the most abundant or rare species are treated below (see Rare species and taxocenoses).

Analysing and comparing habitat characteristics of the water bug species given in Table 10 with both abiotic and biotic characteristics of the lakes, we can state that these habitat characteristics fully or partly match the characteristics of habitats and microhabitats of the lakes. These fishless water bodies represent usable environment for (re)colonisation by vagile stenotopic water bugs preferring meso- to oligotrophic waters, as well as by eurytopic species. Thus, only dramatic negative changes in food offer or habitats should be barriers for long-term (re)colonisation of the lakes.

## Notes to species found in inlets and outlets

Five species of water bugs were found in lakes outlets: *Glaenocorisa propinqua*, *Sigara nigrolineata*, *Notonecta glauca*, *Gerris lacustris*, and *Velia caprai*; the latter was a single species found in inlets (Table 9). *G. propinqua* is exclusively lentic species. *S. nigrolineata* occurs primarily in lentic shallow waters but it is known also from lotic habitats with a negligible current velocity. Similarly, *N. glauca* and *G. lacustris* primarily inhabit lentic waters (or their surface in the case of *G. lacustris*), but they are also known from slowly running parts of lotic habitats or their backwaters (for reviews, see SAVAGE 1989, KMENT 2001). Relatively quickly running waters of lakes outlets are not typical habitat for all these species. *G. lacustris* can colonise more frequently backwaters of outlets. In my opinion, stream backwaters below the lakes (ca. 1 km downstream) are mostly so small that their size is insufficient for successful development (due to intraspecific competition, cannibalism) of this species. The species mentioned above inhabit only (the former two) or primarily (the latter two) still waters or their surface; most probably can be accidentally drifted from the lakes downstream to their outlets. In contrast, the water cricket *V. caprai* is a characteristic species of lotic habitats – small streams and rivulets. It normally inhabits shaded water surface of slowly running waters and backwaters (DITRICH et al. 2008). Some specimens can drift from inlets into lakes or colonise lakes by terrestrial upstream movement from outlets (see DITRICH & PAPÁČEK 2009).

## Rare species

Six rare species are known from the lakes, some are considered endangered or vulnerable (see KMENT & VILÍMOVÁ (2005) and the chapter Species protection).

*Cymatia bonsdorffii* is a predaceous bivoltine species that overwinters in imaginal stage. It has North Palaearctic distribution and southern limits of its area run through central Europe (JANSSON 1986, 1995). The Bohemian Forest and Novohradské Hory Mts. represent the southernmost limit of its area (PAPÁČEK & SOLDÁN 1995, 2003, SOLDÁN et al. 1996, PAPÁČEK 2004). This species inhabits different types of stagnant waters, mostly oligotrophic, mesotrophic and also dystrophic (for review, see KMENT & SMÉKAL 2002). The species was repeatedly collected in Laka Lake that have some shore parts and floating isles formed by peat moss. UNGERMANNOVÁ (2009) found a single specimen of *C. bonsdorffii* also in Grosser Arbersee. This species is also known from the Rokytská Slat' mire in the Bohemian Forest (PAPÁČEK & SOLDÁN 1995) and two localities of the Novohradské Hory Mts. (PAPÁČEK 2002; this area is geographically adjacent and geomorphologically closely related to the Bohemian Forest).

*Glaenocorisa propinqua* is a predaceous pelagic univoltine or somewhere maybe partly bivoltine species overwintering in imaginal stage. This boreo-alpine species with disjunctive distribution (see JANSSON 1986, 1995) occurs in deep oligo- to mesotrophic lakes including artificial ones in central Europe. AUKEMA (pers. comm.) observed the species also in smaller water bodies with depth of about two meters and sandy bottom in the Netherlands. It is highly acid-tolerant, can survive and reproduce at pH round 3 (see WÖLLMANN 2000), and is probably tolerant to changing water chemistry (for review, see KMENT 2001). *G. propinqua* was found to be the dominant and top invertebrate predator in acidified fishless lakes in Scandinavia (HENRIKSON & OSCARSON 1981). Structure and dynamics of its populations is not influenced directly by acidity but indirectly affected by food availability, food web structure, and habitat characteristics (HENRIKSON & OSCARSON 1981, PAPÁČEK & SOLDÁN 1995).

For the first time, *G. propinqua* was recorded from Deschenitzer See (a historical name of Černé Lake; F.A. Kolenati leg.) sub *Corisa carinata* by FIEBER (1848; cf. ROUBAL 1957, JANS-

**Table 11.** Selected characteristics of a structure of true water bug taxocenoses in the littoral zone of four Bohemian Forest lakes (see Table 1 for their codes); shares (%) of species imagines in semiquantitative samples from the 2008 season (modified data from TEXLOVÁ 2010).

Species / Lake	CN	CT	PL	PR
<i>G. propinqua</i>	8	<2	<1	5
<i>S. distincta</i>	2.6	23	<1	10
<i>S. falleni</i>	<1	<1	<1	5.8
<i>S. fossarum</i>	44	17	<1	29
<i>S. nigrolineata</i>	43	56	98	46
Other spp.	1.4	1	< 1	4.2
Index of diversity	1.126	1.068	0.091	1.442
Index of equitability	0.513	0.663	0.044	0.684

SON 1986). FRIČ & VÁVRA (1897) noted large swarms of *Glaenocoris* in Černé and Čertovo lakes. ROUBAL (1957) reviewed literature data on findings of this species from 1884 to 1957. JANSSON (1986) designated a specimen from Plešné Lake as neotype of *G. propinqua*. In the 1990s and 2000s, the species was collected only individually or several specimens (PAPÁČEK & SOLDÁN 1995, 2003, SOLDÁN et al. 1996, PAPÁČEK, unpubl.) in the littoral zone of the studied lakes, as well as in the western part of the Krušné Hory Mts. (KMENT & SYCHRA, unpubl.). KUBEČKA et al. (2000) detected swarms of *Glaenocoris* also by echo-sounder and ichthyoplankton net in the pelagial of Prášílské Lake and the Josefův Důl reservoir (Jizerské Hory Mts.). Recent sampling by series of water light traps, placed in transects at different depth, carried out within a study on spatio-temporal distribution of *G. propinqua*, has shown that the species occurs in Černé, Čertovo, Laka, Plešné, and Prášílské lakes at high population densities (PAPÁČEK, unpubl.). Populations of *G. propinqua* are so numerous that the species can play same role of the top invertebrate predator in the lake communities as in acidified Scandinavian lakes (HENRIKSON & OSCARSON 1981).

*G. propinqua* is a pelagic species; both imagines and nymphs live in open water. This is different behaviour in comparison with most other water boatmen that prefer to live on aquatic plants or at shallow free stony substrates. Consequently, it is relatively difficult to collect *G. propinqua* in the littoral zone. Thus, sampling of this species in the littoral zone and open water by different methods bring quite different results. A single female was found in Grosser Arbersee by a hand net in 2007 (PAPÁČEK, unpubl.). Two nymphs of the species were collected with plankton net in Rachelsee in 2010 (J. Vrba leg., M. Papáček det.). These are the first and solitary records of *G. propinqua* from the German lakes. PETR & PAPÁČEK (2006) suggested that very good flight ability of this species is responsible for its outstanding dispersal potential. Thus, occurrence of *G. propinqua* in Kleiner Arbersee is very likely, as well. This is also supported by finding of one male and two nymphs of *G. propinqua* in a man-made pond, Žďárské Jezírko (960 m a. s. l.; 48°56'N, 13°39'E) in the Bohemian Forest in 2010 and 2011 (PAPÁČEK, unpubl.). Contrary to the lakes, this pond is inhabited by a numerous population of insectivorous fish (stocked brown trout) and water bugs are relatively rare there.

*Sigara semistriata* is a Transpalaeartic faunistic element. It is phyto- to omnivorous bivoltine species overwintering in imaginal stage (KMENT 2001). Although distributed in different freshwaters (JANSSON 1986, 1995, WRÓBLEWSKI 1980, SAVAGE 1989, KMENT 2001), its densities are low. HENRIKSON & OSCARSON (1981) and WOLLMANN (2000) recorded this species together with *G. propinqua* in highly acidified waters. Its occurrence in six lakes (Tables 9, 10) is not surprising.

Two rare yellowish coloured backswimmers, *Notonecta lutea* and *N. reuteri* are predaceous univoltine species overwintering in the egg stage, unlike other central European *No-*

*tonecta* species. Their occurrence is very sporadic in the Czech Republic; however, *N. lutea* has been usually sampled at relatively high frequency in southern parts of south and west Bohemia (PAPÁČEK 2004). Both species are primarily tyrphophilous but they have wider ecological range (especially *N. lutea*; for review, see KMENT & SMÉKAL 2002). Both species occur syntopically in pits of peat bogs in the Bohemian Forest; however, individual findings are also known from localities of different type (KMENT & SMÉKAL 2002, PAPÁČEK 2004). *N. lutea* is a Transpalaeartic species (POLHEMUS 1995b). It was found repeatedly only in Laka Lake and Grosser Arbersee with large peat moss habitats their littoral (Figs. 8, 10). *N. reuteri* is a North Palaeartic species (POLHEMUS 1995b) and glacial relict in central Europe (KMENT & SMÉKAL 2002). The single specimen of *N. reuteri* found in Černé Lake represents a “stepping stone” of the species distribution outside the area of its stable occurrence. Similar single findings of the species in “atypical” localities are known also from the Novohradské Hory Mts. (see PAPÁČEK 2004).

The semiaquatic bug *Gerris lateralis* is a species with boreo-alpine distribution, yet rarely found also in lowlands. This water strider produces only one, mainly macropterous generation per year in colder regions or localities, whereas two generations in the warmer ones. It occurs mainly in “marginal” habitats, where it escapes the competition of other pond skater species (KMENT & SMÉKAL 2002, JEZIORSKI et al. 2012). *G. lateralis* was found only in one (Plešné Lake) of the lakes. It is relatively abundant in some parts of the Novohradské Hory Mts. (PAPÁČEK 2004, DITRICH et al. 2008, JEZIORSKI et al. 2012). Since imagines of the macropterous morph have good vagility, the occurrence of *G. lateralis* in (eastmost) Plešné Lake is not surprising. At least scarce occasional occurrence can be supposed in all remaining Bohemian Forest lakes.

#### Taxocenoses

*Glaenocoris propinqua* is eudominant species of water bug taxocenoses in the Bohemian Forest lakes. As mentioned above, its abundance and dominance is the highest in samples from open water column, i.e. in “pelagic taxocenoses”, where the species is occasionally accompanied by *Callicorixa praeusta*, *Paracorixa concinna*, and *Sigara distincta*. Occurrence of other water bug species is extremely rare in these taxocenoses.

Water bug taxocenoses of the littoral zones of four Bohemian Forest lakes were described by TEXLOVÁ (2010). *Sigara nigrolineata* represents a eudominant to dominant species of these “littoral taxocenoses” (Table 11). It is a West Palaeartic faunistic element, eurytopic species with outstanding migration ability. It inhabits different types of waters, including oligotrophic mountain limnocrenes, rain puddles, and peat bog pits, but mostly avoiding habitats with strong competition of other corixid species (KMENT 2001, PAPÁČEK & SOLDÁN 2003). Other species prevailing in this taxocenoses are as follows: *S. distincta*, a Transpalaeartic species preferring open, deeper and colder waters; *S. falleni*, a Transpalaeartic faunistic element, eurytopic species preferring eutrophic waters, quite common and probably most abundant water boatman in the Czech Republic; and *S. fossarum*, a Holarctic species inhabiting different types of waters including ditches. Specimens of *G. propinqua* represent only a small part of samples from the littoral zones (cf. Table 11).

The least difference between the structure of “pelagic” and “littoral” taxocenoses was found in the most species-rich (22 species) Laka Lake with distinct morphology (Table 1) and diverse microhabitats (stony, sandy, swampy, peaty places of the bottom, littoral plants, floating isles, etc.).

It is apparent that recent taxocenoses of the lakes are predominantly composed of Corixidae (Tables 10, 11). Most of the corixids forming these taxocenoses are detriti-, herbi-, or omnivorous, depending on the food accessibility. *Glaenocoris propinqua*, *Callicorixa*

*praeusta*, scarce *Corixa dentipes* and *C. punctata* (Corixidae), are predaceous species as well as all *Notonecta* species (Notonectidae), or *Plea minutissima* (Pleidae). Specimens of another two predators, *Nepa cinerea* (Nepidae) and *Ilyocoris cimicoides* (Naucoridae) were found only in Laka Lake. All species of semiaquatic bugs are also carnivorous, i.e. predators to scavengers (for review, see SAVAGE 1989, PAPÁČEK 2001).

#### Voltinism and life cycles

Reproduction of water bugs in the Bohemian Forest lakes starts approximately four to six weeks later compared to lowland populations of the same species. This is caused by more severe climatic conditions. Low temperatures and long “dark period”, due to long ice and snow cover in the studied lakes, accelerate the beginning of overwintering, slow down sexual maturation, and delay the beginning of mating and oviposition of water bug populations in spring. In addition, lower water temperatures during summer also extend preimaginal development. This evidence is based on phenology (analysis of samples during spring, summer, and autumn), as well as brief examination of gonad development (maturation) in selected species of water bugs living in the lakes.

Generally in temperate zone, the first (spring) generation of bivoltine corixids maturing before or around summer solstice can mate and produce the second (summer) generation, which reproduces after overwintering in the next spring (YOUNG 1965, 1978, JANSSON & SCUDDER 1974, JANSSON 1986, SAVAGE 1989). In the Bohemian Forest lakes, the less favourable environmental conditions postpone the start of oviposition of both bivoltine and univoltine corixids to the end of May or even June. Preliminary results of our field observations, phenologic analyses of samples, and gonad examination show that the oviposition period of overwintering females is long (live eggs were found also during July). Hatching of the youngest nymphs begins in the first half of June. Only one blunt round and low peak of nymph occurrence was found during summer season. Older nymphs of commonly bivoltine corixids occur still through September. Emergence of the first newly ecdysed imaginal stages were noted relatively late, in the second half of July. Thus, the corixid species that are recorded as bivoltine in lowlands (e.g., *S. nigrolineata* and *S. fossarum*) are univoltine or only partly bivoltine under the conditions of the Bohemian Forest lakes. NIESER (1981) noted similar findings from the Tyrolean water bodies located at 1200–1300 m a.s.l. and higher.

Light, slowly moving nymphs of the 4<sup>th</sup> and 5<sup>th</sup> instar of univoltine, relatively large species *Notonecta glauca*, *Corixa dentipes*, and *C. punctata*, overwintering in the adult stage, were found also during whole October every year. Yet it is questionable if their preimaginal development is finished successfully or not.

#### Changes of taxocenoses during the past two decades

Except for some species, true water bugs (Nepomorpha) are not “true” benthic organisms. Their hard cuticle and way of air breathing from extra body air bubble removable on water surface are generally good predispositions for acidotolerance. Predaceous semiaquatic bugs living on the water surface are even more independent on water quality. Specimens of the Gerridae sampled in the lakes were mostly macropterous (adults and older nymphs). It indicates that they can well migrate and do not have necessarily tight relations to a lake.

Excluding samples of semiaquatic bugs and comparing only samples of true water bugs from the beginning and the end of the 1990s (occasional, from littoral zones only) and from the period of 2007–2011 (semiquantitative or quantitative), we can estimate that the recent taxocenoses of aquatic Heteroptera are more numerous and species-rich and have somewhat different structure than twenty years ago. Some water bug species, found only in one, two or three lakes in the 1990s, have recently been recorded from more lakes (Tables 9, 10). Field

investigations of water bug fauna had different intensity in Czech and German lakes, as well as in the early 1990s and in 2007–2011. The water bug fauna were most intensively investigated in the Czech lakes during 2007–2011. Despite the different research intensity compared to the early 1990s, eight true water bug species and two semiaquatic bug species were newly recorded till 1999. Furthermore, comparing to 1999, twelve true water bug species (Nepomorpha) and six semiaquatic bug species (Gerromorpha) were newly recorded from the Bohemian Forest lakes recently in 2011. It means that nearly 53% of species of recent water bug fauna (52% of nepomorphan and 54% of gerromorphan species) were newly found in the lakes during the past decade. All these species were found in the littoral zone. Newly found species are eurytopic or relatively eurytopic (e.g., *Sigara falleni*, *S. striata*), as well as stenotopic (e.g., *Notonecta reuteri*), including rare species (*N. reuteri*, *Gerris lateralis*). Findings of the lesser water boatman *Micronecta scholtzi* in Černé Lake (total 2 macropterous females, 2 nymphs; 2010, 2011) were surprising. It is commonly known as inhabitant of eutrophic waters, not acidotolerant, and distributed mainly in lowlands; yet it is rarely recorded from saline and dystrophic waters as well (KMENT 2001). Findings of the pygmy backswimmer *Plea minutissima* (Plešné and Prášílské lakes) and the creeping water bug *Ilyocoris cimicoides* (Laka Lake) are also interesting. Although adults of these water bugs (common and widely distributed in eutrophic waters in lowlands) are macropterous, they are mostly considered as flightless by heteropterologists, due to poorly developed flight muscles.

Possible reasons of the above mentioned changes are discussed below (Tracking trends of recovery of Ephemeroptera, Plecoptera, Trichoptera, and Heteroptera in past two decades).

### **Alderflies (Megaloptera) and aquatic Netwingflies (Neuroptera) – T. Soldán & J. Bojková**

Note to contemporary nomenclature

According to recent knowledge, the “Megaloptera” as defined originally seem to be a rather artificial group, probably not of monophyletic origin. Within the Megaloptera *sensu lato*, there are two apparently different taxa clearly defined by a number of autapomorphies (e.g., some characters of mouthparts, musculature and skeletal morphology, abdominal terminalia and types of ovarioles), namely Sialina and Corydalina. Our contribution in fact refers only to the taxon (order) Sialina comprising the family Sialidae. However, since in all papers dealing with insects of lakes and in hydrobiological literature in general the taxon Megaloptera is being still largely used, we did so as well, delimiting the order Megaloptera rather in historical meaning. Similarly, aquatic Neuroptera are frequently called Planipennia in some higher classifications and ecological contributions as well (e.g., BULÁNKOVÁ 2003a). In fact, the families Sisyridae and Osmylidae belong to the suborder Osmyloidea, the only higher taxon with aquatic representatives.

Distribution and biology of Megaloptera (*Sialis*)

Only two species of alderflies, *Sialis lutaria* and *S. fuliginosa* have been found in the Bohemian Forest lakes and outlets, rarely in some inlets (Table 12). The former has been found as early as at the turn of the 19<sup>th</sup> century in Černé Lake (FRÍČ & VÁVRA 1897) and Grosser Arbersee (KLAPÁLEK 1903). Unfortunately, more data are available only after 2000. Only four species of the order have been so far recorded from the Czech Republic (VAŇHARA 1970, 1980, ZELENÝ 1977, ZELENÝ & SEDLÁK 1980, PREISLER & ŠPAČEK 2001, CHLÁDEK 2003). Remaining species, *S. nigripes* Pictet, 1865 and *S. morio* Klingstedt, 1932 belong to critically endangered species (ZELENÝ 2005) and there are no data on their occurrence in the Bohemian Forest, which is rather unlikely, particularly at high altitudes.

**Table 12.** Species of alderflies (Megaloptera) and aquatic netwingflies (Neuroptera) found in the Bohemian Forest lakes in 1897–2010. Species collected in the lakes (see Table 1 for their codes) are in bold; occurrence in individual habitats is distinguished to findings in a lake (L), its inlets (I) and outlet (O); references to unpublished records are not in small caps, i.e., refer to the collector(s) and the year of finding(s).

Family /Species	CN	CT	PL	PR	LA	GA	KA	RA	References
<b>Megaloptera</b>									
<b>Sialidae</b>									
<i>Stialis fuliginosa</i> (Pictet, 1836)	L	L,O				I,O	O	O	Jezberová 2002
	L,O	L,O	O	O	O	I,O	O		SENOO 2009; UNGERMANOVÁ 2009
	L	L,O		O		I	O		Soldán 2010
	L								FRIC & VÁVRA 1897 KLAPÁLEK 1903
<i>Stialis lutaria</i> (Linnaeus, 1758)						L		L	SCHÖLL 1989
	L	L		L	L				Chvojka 1991
	L	L,O	L,O	L	L	L,O	L,O	I,L,O	Jezberová 2002
	L	L,O	L,O	L,O	L,O	L,O	L	L	SENOO 2009; UNGERMANOVÁ 2009
<i>Stialis lutaria</i> (Linnaeus, 1758)	L	L,O	L,O	L,O	O	L,O	L,O	O	Soldán 2010
<b>Neuroptera</b>									
<b>Sisyridae</b>									
<i>Sisyra nigra</i> [sub <i>S. fuscata</i> (Fabricius, 1793)]									
<b>Total number of species</b>	<b>2</b>	<b>2</b>	<b>2</b>	<b>2</b>	<b>2</b>	<b>3</b>	<b>2</b>	<b>2</b>	KLAPÁLEK 1903
Number of species in lakes	2	2	1	1	1	2	1	1	
Number of species in outlets	1	2	2	2	2	2	2	2	
Number of species in inlets	0	0	0	0	0	1	0	1	
Number of species in inlets and outlets	1	2	2	2	2	2	2	2	

The larvae of *S. lutaria* live in ponds, lakes and sluggish parts of streams and rivers, where silt is abundant. They occur in the littoral, sub-littoral, and sometimes also the profundal zones of lakes, even at the depths of 7–20 m, e.g., in Scandinavian (BERG & PETERSEN 1956) or Alpine (DU BOIS & GEIGY 1935) lakes. All instars do not have the same distribution on the bottom. The larvae in their first year are most abundant in the littoral whereas the larger larvae in their second year in the sub-littoral or profundal zones, except when they migrate inshore before pupation in spring (DU BOIS & GEIGY 1935, BERG & PETERSEN 1956, DALL 1987). The life cycle (10 larval instars) usually takes about two years but a longer period of three years has been recorded in lakes at high altitudes, e.g. in Switzerland (GEIGY & GROBE 1958). Although the life cycle span was not studied in detail in the Bohemian Forest lakes, a semivoltine (two year) life cycle can be expected taking into account relative low water temperature and a long period of ice cover (usually from November till late April). Larvae of both species (at least those sampled in late spring and late summer) have two distinguishable size cohorts that might represent one-year- and two-year-old larvae. The univoltine life cycle lasting only one year, with very rapid growth in autumn was observed, e.g., in Denmark (IVERSEN & THORUP 1987).

Contrary to *S. lutaria*, larvae of *S. fuliginosa* seem to be limited to moderately fast-flowing streams and the upper reaches of rivers (HÖLZER et al. 2002, ELLIOT 2009). Its life cycle takes usually two years (KAISER 1961). Analogical habitat preferences of these two species are in the Bohemian Forest at present: *S. fuliginosa* was collected in 2 lakes, all 8 outlets and a single inlet, while *S. lutaria* inhabited all 8 lakes, 7 outlets and a single inlet (Table 12). Our data show a clear preference of the former species for running waters like in other places, where the habitat preference have been studied (HÖLZER et al. 2002, ELLIOT 2009). There are evidently some places, where larvae of the both species live together in the same mesohabitats. If occurring together at the same place, larvae of *S. lutaria* were far more abundant than those of *S. fuliginosa*. This was well apparent not only in the lake littoral but also in outlets. For instance, in the outlet of Čertovo Lake, generally showing a relatively high density of *Sialis* larvae, 75% and 90% of them belonged to *S. lutaria* in late spring and late summer, respectively. However, nearly nothing is known about possible competition between the both species (ELLIOT 2009) and a study of their spatial distribution is needed.

Both species are considered acid-resistant, also viable in permanently acidic streams (LARSEN et al. 1996, BRAUKMANN 2001). *S. lutaria* belongs to taxa often found in acid-stressed lakes negatively aligned along the pH gradient in Swedish lakes (JOHNSON et al. 1993). Similarly, KRNO et al. (2006) considered this species an indicator for strongly acidified lakes in the Tatra Mts. Although our data on the earlier occurrence of *S. lutaria* are limited (Table 12), one can suppose that it occurred in the Bohemian Forest lakes continually and survived all acidification events.

#### Distribution and biology of aquatic Neuroptera (*Sisyra*)

Concerning the aquatic Neuroptera, the only record was published by KLAPÁLEK (1903) who found *Sisyra nigra* (sub *Sisyra fuscata* (Fabricius, 1793)) in Grosser Arbersee (Table 12). According to literature data (HÖLZER et al. 2002, WEISSMAIR 1994, 1999), this species possesses a relatively wide ecological range, occurring in running waters including artificial ones, lakes and fishponds. It is quite possible, however, that this and related species have escaped our attention since the sampling methods currently used in the lakes are not suitable to detect larvae. They inhabit and feed on freshwater sponges (Spongillidae) and bryozoans. The former undoubtedly colonised the lakes in the past, as documented by finding of *Spongilla lacustris* Linnaeus, 1758 in Černé and Čertovo lakes (FRIČ & VÁVRA 1897). Since then, there are no reliable data on the occurrence of freshwater sponges in the Bohemian Forest lakes.

*Sisyra* species mostly occurs at lower altitudes up to about 600 m, montane habitats are colonised quite exceptionally (WEISSMAIR 1994, 1999). This may not be true within the Bohemian Forest, where three species live at relatively high altitude (900–1000 m). *Sisyra terminalis* Curtis, 1854 occurs, e.g., in an impoundment near Knížecí Pláně (PAPÁČEK & SOLDÁN 2003). ZELENÝ (2004b) reported this species from the Chalupská Slat' peat bog near Borová Lada and further locality in the Bohemian Forest foothills, where he found also *S. fuscata* (Fabricius, 1793). The occurrence of remaining species of aquatic (semiaquatic) Neuroptera, *Osmylus fulvicephalus* (Scopoli, 1763) in the studied lakes and surrounding habitats is unlikely, as the species usually occurs at lower altitudes. However, besides its relatively abundant distribution in the Bohemian Forest foothills, ZELENÝ (2004b) found this species at the locality of Zátoň near Boubín Mt. Unlike Megaloptera, the sensitivity of *Sisyra* or other aquatic Neuroptera to low pH remains unknown.

### Caddisflies (Trichoptera) – P. Chvojka

The first mention of caddis larvae (“Phryganäenlarven“) from the Bohemian Forest lakes (Černé Lake) can be found in FRIČ (1872). More detailed data were obtained from Černé, Čertovo, Grosser Arbersee, Laka and Plešné lakes later (in the 1890s and 1900s; FRIČ & VÁVRA 1897, KLAPÁLEK 1890, 1894, 1903). Next important records were from the middle of the last century, when caddisflies were collected in the vicinity of some Czech lakes (Černé, Čertovo, Laka, Prášílské; NOVÁK 1996). All eight lakes have been investigated more intensively only during the past two decades.

In total 46 Trichoptera species are known from the Bohemian Forest lakes, 19 of which inhabit the lakes and 32 their inlets and outlets (Table 13). The occurrence of a boreo-montane species, *Molanna nigra*, is particularly remarkable from the point of view of biogeography. The species was recently recorded in Grosser Arbersee, Čertovo, and Prášílské lakes; earlier records are known also from Černé Lake. Several streams above 1000 m a.s.l. in the Bohemian Forest, including inlets of Černé and Laka lakes, represent the only localities of the occurrence of *Drusus chrysotus* and *Acrophylax zerberus* in the Czech Republic (NOVÁK 1996, CHVOJKA et al. 2009).

#### Caddisflies of the lake littoral

In most cases, about 9 species were found in a single lake (maximum 12 and minimum 4 species in Grosser Arbersee and Rachelsee, respectively, Table 13). Different number of species reflects both differences in abiotic conditions of the lakes and attention that has been paid to study of individual lakes. The lowest numbers of species found in Rachelsee and Kleiner Arbersee may result from the combination of very short history of investigation of these lakes and insufficient recent sampling activities.

The most frequent as well as most abundant caddisflies are phryganeids and limnephilids. *Agrypnia varia* was recorded from all lakes, *Phryganea bipunctata* and *Limnephilus rhombicus* from all lakes with the exceptions of Kleiner Arbersee and Rachelsee, respectively. These widespread and rather eurytopic species are known from different types of standing waters, and also from brackish habitats and montane peat bogs (GRAF et al. 2008, CHVOJKA 2008). Further common species is *Oligotricha striata*, which is absent only in Černé and Čertovo lakes. Generally, its larvae can be found in pools, ponds, peat bogs, including strongly acidified waters (WALLACE et al. 1990, WÄRINGER & GRAF 1997, BRAUKMANN & BISS 2004).

Other frequent species are *Cyrnus flavidus*, *Plectrocnemia conspersa*, *Limnephilus centralis*, *Chaetopteryx villosa*, *Molanna nigra*, *Molannodes tinctus*, and *Mystacides azurea*. The larvae of *C. flavidus* live among macrophytes in the littoral zone of lakes and slowly

**Table 13.** Species/taxa of caddisflies (Trichoptera) found in the Bohemian Forest lakes in 1890–2010. Species collected in the lakes (see Table 1 for their codes) are in bold; occurrence in individual habitats is distinguished to findings in a lake “L”, its inlets “I” and outlet “O”; parentheses indicate either imagines from running waters collected around a lake “(L)” or larvae drifted to a lake outlet “(O)”; references to unpublished records are not in small caps, i.e., refer to the collector(s) and the year of finding(s).

Family / Species	CN	CT	PL	PR	LA	GA	KA	RA	References
<b>Rhyacophilidae</b>									
<i>Rhyacophila dorsalis persimilis</i> McLachlan, 1879	I,(L)			O	O				the 1950s (NOVÁK 1996)
					O	O	O		Chvojka 1991
									Chvojka 2007
									SYCHRA et al. 2008
									SVOBODOVÁ 2010
									Bojková 2010
<i>Rhyacophila cf. dorsalis</i> (larvae)		O	O	O	I,O	O	O		Jezberová 2002, 2003
<i>Rhyacophila glareosa</i> McLachlan, 1867									the 1950s (NOVÁK 1996)
					I				Chvojka 1991
					(L)				the 1950s (NOVÁK 1996)
<i>Rhyacophila obliterata</i> McLachlan, 1863		O			O	I	I,O	I	Chvojka 2007
									SYCHRA et al. 2008
		O					I		SENOO 2009
									Bojková 2010
<i>Rhyacophila praemorsa</i> McLachlan, 1879		I			I		O		Jezberová 2002, 2003
							O		SENOO 2009
					I				Bojková 2010
<b>Ptilocolepidae</b>									
<i>Ptilocolepus granulatus</i> (Pictet, 1834)		I			I			I	Chvojka 1991
									SENOO 2009
<b>Philopotamidae</b>									
<i>Philopotamus indificatus</i> McLachlan, 1878					I				ŠAMAL 1920
									Chvojka 2007
<i>Philopotamus montanus</i> (Donovan, 1813)					(L)				ŠAMAL 1920
					O				the 1950s (NOVÁK 1996)
<i>Wormaldia occipitalis</i> (Pictet, 1834)							I	I	Chvojka 2007
		O							Bojková 2010
<b>Polycentropodidae</b>									
<i>Cynus flavidus</i> McLachlan, 1864	L		L				L		KLAPÁLEK 1903
<i>Cynus trimaculatus</i> (Curtis, 1834)	L						L		UNGERMANOVÁ 2009
									KLAPÁLEK 1903

Table 13. Continued

Family / Species	CN	CT	PL	PR	LA	GA	KA	RA	References
<i>Holocentropus dubius</i> (Rambur, 1842)		O		O	L	L			UNGERMANOVÁ 2009
<i>Plectrocnemia conspersa</i> (Curtis, 1834)	I, L	I, L	L	L, O	I				the 1950s (NOVÁK 1996) Chvojka 1991, 1994, 1999
								I	SCHAUMBURG 2000
	I	I, L, O	I, L, O	I, O	I, O	I	I, O	I, O	Jezbetová 2002, 2003
	I, O	I, O	I, O	I, O	I, O	I, O	I, O	I, O	SENCOO 2009; SVOBODOVÁ 2010
			O						Bojková 2010
<i>Plectrocnemia gemiculata</i> McLachlan, 1871		I							Jezbetová 2002
	I	I		I					SENCOO 2009
<i>Polycentropus flavomaculatus</i> (Pictet, 1834)		L	L						KLAPÁLEK 1890, 1903
			L, (O)						Jezbetová 2002
			L						UNGERMANOVÁ 2009
<b>Psychoomyiidae</b>									
<i>Lype phaeopa</i> (Stephens, 1836)						L			KLAPÁLEK 1903
<b>Phryganeidae</b>									
<i>Agrypnia varia</i> (Fabricius, 1793)	L	L	L						KLAPÁLEK 1903
	L								Chvojka 1991, 1999
	L			L	L	L	L	L	Jezbetová 2002, 2003
	L	L	L	L	L	L	L	L	UNGERMANOVÁ 2009
<i>Oligotricha striata</i> (Linnaeus, 1758)				L					the 1950s (NOVÁK 1996)
				L	L				Chvojka 1991, 1994
				L	L				Jezbetová 2002, 2003
				L, (O)	L	L	L	L	SENCOO 2009; UNGERMANOVÁ 2009
				L, (O)	L, (O)	L	L	L	UNGERMANOVÁ 2009
<i>Phryganea bipunctata</i> Retzius, 1783	L	L							FRÍČ & VÁVRA 1897
	L	L				L			KLAPÁLEK 1890, 1903; Klapálek 1891
									SCHÖLL 1989
	L	L	L	L	L			L	Chvojka 1991, 1999
				L, (O)					SENCOO 2009; UNGERMANOVÁ 2009
<i>Phryganea</i> sp. (larva)		(O)							SVOBODOVÁ 2010
<b>Apataniidae</b>									
<i>Apatania fimbriata</i> (Pictet, 1834)									the 1950s (NOVÁK 1996)
				I	I				Chvojka 1991

Table 13. Continued

Family / Species	CN	CT	PL	PR	LA	GA	KA	RA	References
<b>Limnephilidae</b>									
Subfamily Drusinae									
<i>Drusus annulatus</i> (Stephens, 1837)				I	I				Chvojka 1991
				I	I				Jezbetová 2002
				I	I				SENOO 2009
<i>Drusus chrysotus</i> (Rambur, 1842)	I								CHVOJKA et al. 2009
<i>Drusus discolor</i> (Rambur, 1842)	I	I		O					ŠÁMAL 1920
				I	I				SENOO 2009
Subfamily Limnephilinae (Limnephilini)									
<i>Limnephilus centralis</i> Curtis, 1834					L				KLAPÁLEK 1903
									the 1950s (NOVÁK 1996)
								L	SCHÖLL 1989
		I,L							Chvojka 1999
					L				SYCHRA et al. 2008
					I				Bojková 2010
<i>Limnephilus coenosus</i> Curtis, 1834	L								KLAPÁLEK 1903
	L		I						Jezbetová 2002
	L	I	I						SENOO 2009; UNGERMANOVÁ 2009
<i>Limnephilus decipiens</i> (Kolenati, 1848)						L			KLAPÁLEK 1903
<i>Limnephilus lunatus</i> Curtis, 1834				L					ŠÁMAL 1920
<i>Limnephilus nigriceps</i> (Zetterstedt, 1840)						L			Jezbetová 2003
					L	L	L		Chvojka 2007
					L				SYCHRA et al. 2008
					L	L	L		Bojková 2010
<i>Limnephilus rhombicus</i> (Linnaeus, 1758)	L	L	L	L	L	L	L		KLAPÁLEK 1903
	L	L	L	L	L				Chvojka 1990, 1991, 1994
	L		L <sub>2</sub> (O)	L <sub>2</sub> (O)	L <sub>2</sub> (O)	L	L		Jezbetová 2002, 2003
	L	I,L	L <sub>2</sub> (O)	L <sub>2</sub> (O)	L <sub>2</sub> (O)	L	L		SENOO 2009; UNGERMANOVÁ 2009; SVOBODOVÁ 2010
<i>Limnephilus</i> sp. (larvae)	L								FRÍČ & VÁVRA 1897
<i>Rhadicoleptus alpestris alpestris</i> (Kolenati, 1848)	I								Chvojka 2007
		I							SENOO 2009

Table 13. Continued

Family / Species	CN	CT	PL	PR	LA	GA	KA	RA	References
Subfamily Limnephilinae (Chaetopterygini)									
<i>Chaetopterygopsis maclachlani</i> Stein, 1874			(L)						the 1950s (NOVÁK 1996)
				I					Jezberová 2002
				I					Chvojka 2007
	I	I							SENOO 2009
									Bojková 2010
<b><i>Chaetopteryx villosa</i></b> (Fabricius, 1798)	L	L							FRÍČ & VÁVRA 1897
	L								KLAPÁLEK 1894
	L		L	O					the 1950s (NOVÁK 1996)
	L	L	L	L					Chvojka 1991
	I,L	I,L,O	I	I,O	I				Jezberová 2002
	I,L	I	I	I,L,O	I	I,O	I		Chvojka 2007
	I,L	I,L,O	I,L	I,L,O					SENOO 2009; UNGERMANOVÁ 2009; SVOBODOVÁ 2010
	I,L	I,L	I,L	I,L	I,O				Bojková 2010
<i>Pseudopsilopteryx zimmeri</i> (McLachlan, 1876)			I	I					Jezberová 2002
					O				Chvojka 2007
		I	I						SENOO 2009
<i>Psilopteryx psorosa bohemosaxonica</i> Mey et Botosaneanu, 1985			(L)						the 1950s (NOVÁK 1996)
		I							Jezberová 2002
	I	I		I	I	I	I		Chvojka 2007
				I	I	I			Bojková 2010
Subfamily Limnephilinae (Stenophylacini)									
<i>Acrophylax zerberus</i> Brauer, 1867					O				Jezberová 2002
					I				CHVOJKA et al. 2009
	I								Bojková 2010
					I				Chvojka 2007
<i>Allogamus uncatus</i> (Brauer, 1857)					I				Bojková 2010
<i>Halesus rubricollis</i> (Pictet, 1834)					I				BOJKOVÁ 2010
<i>Halesus</i> sp. (larva)					O	(L)			KLAPÁLEK 1890
<i>Hydatophylax infumatus</i> (McLachlan, 1865)									Jezberová 2003
								O	SENOO 2009
					I,O	I			SENOO 2009
<i>Melampophylax nepos nepos</i> (McLachlan, 1880)		O							SVOBODOVÁ 2010

Table 13. Continued

Family / Species	CN	CT	PL	PR	LA	GA	KA	RA	References
<i>Micropterna nycterobia</i> McLachlan, 1875			I						SENCOO 2009
<i>Parachiona picicornis</i> (Pictet, 1834)				I					Chvojka 1991
									Jezberová 2002
	I								SENCOO 2009
							I		Bojtková 2010
<b>Sericostomatidae</b>									
<i>Sericostoma</i> sp. (larva)					O				SVOBODOVÁ 2010
<b>Odontoceridae</b>									
<i>Odontocerum albicorne</i> (Scopoli, 1763)					(L),O				the 1950s (Novák 1996)
					O				Chvojka 1991
					O	O			Jezberová 2002, 2003
					O				SENCOO 2009; SVOBODOVÁ 2010
<b>Molannidae</b>									
<i>Molanna nigra</i> (Zetterstedt, 1840)	L	L				L			KLAPÁLEK 1903
	L			L					the 1950s (Novák 1996)
				L					Chvojka 1991, 1994
						L			WEINZIERL 1999
				L					Jezberová 2002
	L <sub>1</sub> (O)			L <sub>1</sub> (O)		L			SENCOO 2009; UNGERMANOVÁ 2009; SVOBODOVÁ 2010
<i>Molannodes tinctus</i> (Zetterstedt, 1840)					L				Chvojka 1991
					L <sub>1</sub> (O)				Jezberová 2002
					L <sub>1</sub> (O)		L		SENCOO 2009; UNGERMANOVÁ 2009
<b>Leptoceridae</b>									
<i>Mystacides azurea</i> (Linnaeus, 1761)	L	L							Chvojka 1991, 1994, 1999
	L								Jezberová 2002
	L	L <sub>1</sub> (O)				L <sub>1</sub> (O)			SENCOO 2009; UNGERMANOVÁ 2009; SVOBODOVÁ 2010
<b>Total number of species/taxa</b>	<b>18</b>	<b>23</b>	<b>14</b>	<b>23</b>	<b>30</b>	<b>21</b>	<b>14</b>	<b>10</b>	
Number of species in lakes	10	9	9	9	9	12	6	4	
Number of species in outlets	1	6	2	8	10	4	5	2	
Number of species in inlets	10	14	5	13	18	6	6	5	
Number of species in inlets and outlets	10	18	6	17	23	9	8	6	

flowing waters and also in brackish waters (GRAF et al. 2008). It represents an acid-tolerant species with pH optimum 4.8 in Scandinavia (LARSEN et al. 1996). *P. conspersa* is a widespread and common species in rhithral, crenal and also in the littoral zone of mountain lakes (FÜREDER et al. 2006, KRNO et al. 2006, GRAF et al. 2008). It is a very acid-resistant species (BRAUKMANN & BISS 2004) often abundant in acidic or metal-polluted streams (EDINGTON & HILDREW 1995). In the Bohemian Forest lakes, *P. conspersa* occurs not only in the lake littoral but it is indeed the most frequent species of inlets and outlets. *L. centralis* occurs in temporary pools, marshes, ponds and streams (WALLACE et al. 1990); it is common species of wetlands in the Bohemian Forest (NOVÁK 1996) also recorded from several lakes (Table 13). *C. villosa*, a widespread and common species in running waters and mountain lakes with stony substrate and organic debris (WALLACE et al. 1990), is abundant also in streams and lakes of the Bohemian Forest; it is a very acid-resistant species (BRAUKMANN & BISS 2004). Exact requirements of *Molanna nigra* are insufficiently known, other *Molanna* species and also *Molannodes tinctus* inhabit stagnant or slowly flowing water with sandy or muddy substrates (GRAF et al. 2008). These species are probably rather acid-tolerant, e.g., *M. tinctus* survived in Plešné Lake during a period of strong acidification (CHVOJKA, unpubl.). *Mystacides azurea* is common in standing and slowly flowing waters among vegetation, woody debris, roots, and on muddy and sandy bottom; it is known also from brackish waters (GRAF et al. 2008). Its pH optimum is 5.4 in Scandinavia (LARSEN et al. 1996); it was recorded in strongly acidified Černé and Čertovo lakes in the Bohemian Forest. *Limnephilus nigriceps* was collected in littoral sedgy growth in Grosser Arbersee, Kleiner Arbersee, and Laka Lake. Generally, this species can be found in still and slowly flowing waters with emergent macrophytes (WALLACE et al. 1990, GRAF et al. 2008). *Limnephilus coenosus* inhabits pools, marshes, peat-bogs, and lakes at higher altitudes (WALLACE et al. 1990, WARINGER & GRAF 1997, CHVOJKA 2008), it is characteristic for strongly acidified lakes in the Tatra Mts. (KRNO et al. 2006). It was regularly collected in Černé Lake and in some lake inlets. Remaining species listed from the Bohemian Forest lakes were collected only occasionally.

#### Caddisflies of lake inlets and outlets

Altogether 32 species were recorded from lake inlets and outlets; the number of species varies between 23 and 6 in individual lake catchments. This broad range can be again partly affected by unequal attention devoted to these study sites. The most frequent species of inlets and/or outlets are *Plectrocnemia conspersa*, *Chaetopteryx villosa* (both inhabiting also lakes), and *Rhyacophila* spp. (*R. dorsalis*, *R. glareosa*, *R. oblitterata*, *R. praemorsa*). All these species are widespread in the study area (NOVÁK 1996); they are known from periodically strongly acidic streams (BRAUKMANN & BISS 2004). Another common species is *Psilopteryx psorosa* which is missing only in inlets of Plešné Lake. Its larvae live in rhithral zone (GRAF et al. 2008). This species is considered an indicator of neutral to episodically weakly acidic streams (BRAUKMANN & BISS 2004); however, it occurs also in strongly acidified streams in the Bohemian Forest. *Drusus discolor*, *Chaetopterygopsis maclachlani*, *Pseudopsilopteryx zimmeri*, and *Parachiona picicornis* are also frequent in lake inlets, all these species belong to acid-resistant aquatic insects (BRAUKMANN & BISS 2004).

The highest diversity of caddisflies (23) was recorded from inlets and outlet of Laka Lake (Table 13). *Philopotamus ludificatus*, *Sericostoma* sp., and *Allogamus uncatatus* has been found only in the Laka catchment, the former species is classified as a moderately acid-sensitive, two latter as acid-tolerant and acid-resistant species, respectively. Other species recorded (*Apatania fimbriata*, *Drusus annulatus*, *Odontocerum albicorne*), present in Laka, Prášílské, and Grosser Arbersee catchments, are considered acid-resistant (BRAUKMANN & BISS 2004).

Although trichopterological investigation in the Bohemian Forest (especially in the Czech part) has got rather long history and caddisfly fauna of this region as a whole has been well documented (cf. NOVÁK 1996), earlier data from individual lakes or their catchments were incomplete or even missing. It is difficult to evaluate long-term changes of caddisfly taxocenoses in connection with the lake acidification, because the species richness found in individual research periods are often influenced by different sampling efforts. Investigations were not extensive in the past, representative data sets based on imagines collections from the turn of the 19<sup>th</sup> and 20<sup>th</sup> century were obtained only from Grosser Arbersee, Černé and Čertovo lakes, while data from Černé, Čertovo, and Prášílské lakes from the 1950s are rather fragmentary. KLAPÁLEK (1890, 1894, 1903) reported 12 species from lakes, of which only *Cyrnus trimaculatus*, *Lype phaeopa*, and *Limnephilus decipiens* have not been re-collected later. The former species is a common species in running and stagnant waters preferring acid ones (LARSEN et al. 1996, GRAF et al. 2008), imagines of the latter were collected in Grosser Arbersee only sporadically. *L. phaeopa* is specialised on the xylal microhabitat (GRAF et al. 2008) and its larvae could be overlooked during recent macroinvertebrate sampling.

More intensive investigations started in the 1990s and regular monitoring, involving the sampling of imagines and larvae of Trichoptera in all the lakes, was carried out only in the last decade and altogether 15 species were found in this period. Several of them (*Holocentropus dubius*, *Plectrocnemia conspersa*, *Oligotricha striata*, *Limnephilus nigriceps*, *Molannodes tinctus*, *Mystacides azurea*) were not found in the past. Absence of *P. conspersa* and *M. azurea* in Černé and Čertovo lakes during pre-acidification period is particularly remarkable; however, we can only hypothesise on the effect of trophic relations in the lakes and fish predation on littoral populations of caddis larvae by natural or introduced populations of salmonids (see VRBA et al. 2003a). Abundance of *P. conspersa* can be greatly reduced due to fish predation as documented by EDINGTON & HILDREW (1995). Similar effect can be supposed in the case of *O. striata*. KLAPÁLEK (1903) surprisingly did not record this species, although the lakes had humic dark brown water at that time (VRBA et al. 2000), which was typical habitat of *O. striata*. Possible changes of caddisfly taxocenoses during recovery of the Bohemian Forest lakes from acidification in the future will follow changes of trophic structure of lakes.

## **Aquatic beetles (Coleoptera) – J. Sychra**

### Species richness of taxocenoses

Altogether 52 species of aquatic and semi-aquatic beetles of 28 genera and 10 families (Gyrinidae, Haliplidae, Noteridae, Dytiscidae, Helophoridae, Hydrophilidae, Hydraenidae, Scirtidae, Elmidae, Chrysomelidae) have been found in eight Bohemian Forest lakes (Table 14). Such a high species richness is more comparable to rather oligotrophic lakes and ponds of moderate altitude (e.g., FAIRCHILD et al. 2003, TOUAYLIA et al. 2011) than to boreal or alpine lakes in central Europe, which usually show considerably lower species richness (cf. KOWNACKI et al. 2000, BOGGERO & LENCIONI 2006, FÜREDER et al. 2006, KRNO et al. 2006, OERTLI et al. 2008). Similar number (54 taxa) of beetle species was found only within the survey of 95 Tatra lakes in the alpine zone (ČIAMPOROVÁ-ZAŤOVIČOVÁ & ČIAMPOR 2011) compared to our 8 lakes. However, for more accurate comparison, studies focused to aquatic insects of similar mountain lakes situated in the forest zone about 1000 m a.s.l. are extremely scarce. Generally, taxa diversity of aquatic beetles is negatively correlated with altitude, which is probably due to lower temperature and absence of macrophyte beds and organic substrate at higher altitudes (HOFFMAN et al. 1996, HEINO 2008, ČIAMPOROVÁ-ZAŤOVIČOVÁ & ČIAMPOR 2011, TOUAYLIA et al. 2011). On the other hand, an inverse pattern of species richness

ss has been documented at lower altitudes, caused by the negative impact of fish due to both food competition and predatory pressure on aquatic beetles (KOWNACKI et al. 2000, DE MENDOZA & CATALAN 2010). This is not the case of the Bohemian Forest lakes, where fish did not occur during the past 50 years.

The most abundant taxa of aquatic beetle taxocenoses inhabiting the lakes are typical also for alpine lakes across the Holarctic region. The presence of characteristic dytiscid species of the genera *Agabus*, *Hydroporus*, and some potamal species of Hydroporini (most frequently genera *Deronectes*, *Nebrioporus* or *Stictotarsus*) is typical (HOFFMAN et al. 1996, KOWNACKI et al. 2000, FÜREDER et al. 2006, KRNO et al. 2006, OERTLI et al. 2008, ČIAMPOROVÁ-ZAŤOVIČOVÁ & ČIAMPOR 2011). Most recorded species were eurytopic (acid-tolerant) or acidophilous, which was consistent with known aquatic beetles fauna of surrounding habitats of the Bohemian Forest with many acidic streams, wetlands, and bogs (PETR 2000, VALENTA & SOLDÁN 2001, SYCHRA et al. 2008). Species with Palaearctic or European type of distribution (some of them Holarctic) prevailed in the surveyed taxocenoses.

### Impact of acidification

There is virtually no information about long-term changes in the composition of aquatic beetle taxocenoses in the Bohemian Forest lakes. In the first research of these lakes, FRIČ & VÁVRA (1897) found only 3 species in Černé and Čertovo lakes: *Gyrinus substriatus* (sub *G. nator*; this name was commonly used as synonym for *G. substriatus* in earlier publications, BOUKAL et al. 2007), *Hydroporus palustris*, and *Deronectes latus* (sub *Hydroporus latus*). Only very scarce records of aquatic beetles come from the second half of the last century concerned two additional dytiscid species, *Agabus guttatus* and *Hydroporus memnonius* (HÁJEK in litt.). All other data on any of 52 species recorded in total originate from the first decade of this century and included also those 5 historically recorded species from the same localities (Table 14). The only faunistic research targeted directly to aquatic beetles of the Bohemian Forest lakes was performed during May and September 2010. Altogether 47 species have been found, including 29 species recorded from these lakes for the first time.

Consequently, existing data do not provide any possibility to evaluate the impact of acidification of lakes on this insect group. Moreover, invertebrates with high and rapid dispersal ability, such as many aquatic beetles and true bugs of standing waters, are generally not suitable for monitoring of long-term changes at particular sites. Aquatic beetles are not good indicators of acidification or recovery from acidification, since there are only a few acid-sensitive aquatic beetles (JULIANO 1991, FOSTER 1995, ARNOTT et al. 2006), especially at higher altitudes, although lower pH can induce behavioural changes of some species (CALOSI et al. 2007). In running waters inhabited by less mobile species and those closer related to particular site, an apparent response of aquatic beetles to acidification was documented (BRAUKMANN 2001). On the contrary, many species recorded in the Bohemian Forest lakes are typically acidophilous (e.g., *Hydroporus memnonius*, *H. obscurus*, *H. tristis*, *Agabus sturmii*, *A. affinis*, *A. melanarius*, *Helophorus flavipes*, *Enochrus ochropterus*, *E. affinis*). In addition the abundance of some predatory aquatic insects can even increase with decreasing pH, which can be caused by the absence of competing fish predators (CARBONE et al. 1998).

### Characteristics of lake littoral and aquatic beetle fauna

Aquatic beetles are mostly dependent on characteristics of the littoral zones, where their diversity and abundance are highest in comparison with other habitats of the lake. The presence and extent of aquatic plant beds positively influence food quality and availability, li-

**Table 14.** Species of aquatic beetles (Coleoptera, imagines) found in the Bohemian Forest lakes in 1872–2011. Species collected in the lakes (see Table 1 for their codes) are in bold; occurrence in individual habitats is distinguished to findings in a lake (L), its inlets (I) and outlet (O); references to unpublished records are not in small caps, i.e., refer to the collector(s) and the year of finding(s).

Family / Species	CN	CT	PL	PR	LA	GA	KA	RA	References
<b>Gyrinidae</b>									
<i>Gyrinus (Gyrinus) marinus</i> Gyllenhal, 1808								L	Sychra 2010
<i>Gyrinus (Gyrinus) substriatus</i> Stephens, 1828	L	L							FRÍČ 1872 <sup>1)</sup> ; FRÍČ & VÁVRA 1897 <sup>1)</sup>
	L								Hervert 1977
	L			O					Jezberová 2002
	L,O	L		L				L	Papáček 2007; Sychra 2010
<b>Halipilidae</b>									
<i>Halipilus (Halipilus) heydeni</i> Wehncke, 1875								L	Sychra 2010
<i>Halipilus (Halipilus) sibiricus</i> Motschulsky, 1860				L	L				Papáček 2011
<i>Halipilus (Liaphilus) flavicollis</i> Sturm, 1834			L	L					Papáček 2007, 2010
<b>Noteridae</b>									
<i>Noterus clavicornis</i> (De Geer, 1774)				L			L		Sychra 2010; Papáček 2011
<i>Noterus crassicornis</i> (O.F. Müller, 1776)							L		Jezberová 2002
			L	L			L		Papáček 2007; Sychra 2010
<b>Dytiscidae</b>									
<i>Deronectes latus</i> (Stephens, 1829)	L								FRÍČ & VÁVRA 1897 <sup>2)</sup>
	I,L,O	L,O	O	O				O	Jezberová 2002; Soldán 2002
	I,L	L,O	L,O	I,O			O	O	Papáček 2009; SVOBODOVÁ 2010; Sychra 2010
<i>Deronectes platynotus platynotus</i> (Germar, 1836)		O			O	I		O	Jezberová 2002; Soldán 2002
	O				O	I		O	SVOBODOVÁ 2010; Sychra 2010
				L,O					Sychra 2010
<i>Graptodytes pictus</i> (Fabricius, 1787)			L	L	L	L		L	Sychra 2010
<i>Hydroglyphus geminus</i> (Fabricius, 1781)			I						Jezberová 2002
<i>Hydroporus erythrocephalus</i> (Linnaeus, 1758)			L						Papáček 2009; Sychra 2010
<i>Hydroporus ferrugineus</i> Stephens, 1828				I					Jezberová 2002
	I	I	I	I	I				Sychra 2010
<i>Hydroporus incognitus</i> Sharp, 1869			L	L	L				Sychra 2010
<i>Hydroporus memnonius</i> Nicolai, 1822		L							Jelínek 1991
	I								Jezberová 2002
<i>Hydroporus nigrita</i> (Fabricius, 1792)	L	I	I		I,L	L	L	L	Soldán 2009; Sychra 2010
<i>Hydroporus obscurus</i> Sturm, 1835					L				Sychra 2010
							L		Sychra 2010

Table 14. Continued

Family / Species	CN	CT	PL	PR	LA	GA	KA	RA	References
<i>Hydroporus palustris</i> (Linnaeus, 1761)	L								FRÍČ 1872; FRÍČ & VÁVRA 1897
	L								Doležal 1974
	L	L	I,L,O		L				Jezberová 2002; Soldán 2002
	I,L,O	I,L,O	I,L,O		L	I,L	L	I,L	SYCHRA et al. 2008; Soldán 2009; Papáček 2009, 2011; Sychra 2010
<i>Hydroporus planus</i> (Fabricius, 1781)					L				Sychra 2010
<i>Hydroporus tristis</i> (Paykull, 1798)			L	L,O	L		L		Sychra 2010
<i>Hydroporus umbrosus</i> (Gyllenhal, 1808)			L						Sychra 2010
<i>Hygrotes (Coelambus) impressopunctatus</i> (Schaller, 1783)	L						L		Sychra 2010
<i>Hygrotes (Hygrotes) versicolor</i> (Schaller, 1783)							L		Jezberová 2002
<i>Hyphydrus ovatus</i> (Linnaeus, 1761)					L		L		Sychra 2010
<i>Nebrioporus (Nebrioporus) assimilis</i> (Paykull, 1798)				L,O					Papáček 2007, 2011; Sychra 2010
<i>Oreodytes sammarkii</i> (C. R. Sahlberg, 1826)				O			I		Jezberová 2002
<i>Agabus (Acatodes) sturnii</i> (Gyllenhal, 1808)						L			Jezberová 2002
			L	I,L	L	L	L	I,L	Papáček 2007; SYCHRA et al. 2008; Soldán 2009; Sychra 2010
<i>Agabus (Gaurodytes) affinis</i> (Paykull, 1798)					L	L			Sychra 2010
<i>Agabus (Gaurodytes) biguttatus</i> (Olivier, 1795)	L			L	I,L				Sychra 2010
<i>Agabus (Gaurodytes) bipustulatus</i> (Linnaeus, 1767)									Doležal 1974
<i>Agabus (Gaurodytes) guttatus guttatus</i> (Paykull, 1798)	I,O	I,L,O	O		I			O	Jezberová 2002; Nytková 2002
	I	I,O	I,O	I	I	I	I	I	Soldán 2009; Sychra 2010
	L								Gahai 2004
<i>Agabus (Gaurodytes) melanarius</i> Aubé, 1837			I	I	I	I	O		Sychra 2010
<i>Ilybius crassus</i> Thomson, 1856				L	L	L	L	L	Sychra 2010
<i>Rhantus (Rhantus) exsoletus</i> (Forster, 1771)						L			Jezberová 2002
			L		L	L	L		Papáček 2007; SYCHRA et al. 2008; Sychra 2010; Papáček 2011
<i>Rhantus (Rhantus) frontalis</i> (Marsham, 1802)			L						Sychra 2010
<i>Rhantus (Rhantus) suturalis</i> (MacLeay, 1825)				L					Sychra 2010
<i>Laccophilus minutus</i> (Linnaeus, 1758)			L				L	L	Sychra 2010
<i>Dytiscus marginalis marginalis</i> Linnaeus, 1758					L				Papáček 2007
Helophoridae									
<i>Helophorus (Rhopalohelophorus) flavipes</i> Fabricius, 1792			O						Jezberová 2002
			L	L,O			L		Sychra 2010

Table 14. Continued

Family / Species	CN	CT	PL	PR	LA	GA	KA	RA	References
<b>Helophorus (Rhopalohelophorus) granularis</b> (Linnaeus, 1761)						L			Sychra 2010
<b>Hydrophilidae</b>									
<i>Cercyon (Cercyon) quisquilius</i> (Linnaeus, 1761)		O							SVOBODOVÁ 2010 <sup>3)</sup>
<i>Coelostoma orbiculare</i> (Fabricius, 1775)					L	L			SYCHRA et al. 2008; Sychra 2010
<i>Anacaena globulus</i> (Paykull, 1798)		I		I,L,O		L			Sychra 2010
<i>Anacaena lutescens</i> (Stephens, 1829)		L	L,O	L,O	L	I,L	L	L	SYCHRA et al. 2008; Sychra 2010
<i>Berosus (Berosus) signaticollis</i> (Charpentier, 1825)			L						Papáček 2011
<i>Enochrus (Lumetus) ochropterus</i> (Marshall, 1802)					L,O	L	L		SYCHRA et al. 2008; Soldán, 2009; SVOBODOVÁ 2010; Sychra 2010
<i>Enochrus (Methyrus) affinis</i> (Thunberg, 1794)						L	L	L	Sychra 2010
<i>Hydrobius fuscipes</i> (Linnaeus, 1758)			L	L		L	L	L	Sychra 2010
<i>Laccobius (Laccobius) minutus</i> (Linnaeus, 1758)			L	L					Sychra 2010; Papáček 2011
<b>Hydraenidae</b>									
<i>Hydraena (Hydraena) brittani</i> Joy, 1907					L				Sychra 2010
<b>Scirtidae</b>									
<i>Cyphon padi</i> (Linnaeus, 1758)				L	L	L	L		Sychra 2010
<i>Cyphon punctipennis</i> Sharp, 1872				L				L	Sychra 2010
<i>Cyphon variabilis</i> (Thunberg, 1787)				L	L		L		Sychra 2010
<b>Elmidae</b>									
<i>Elmis rtioloides</i> (Kuwert, 1890)					O				Sychra 2010
<i>Limnius perrisi perrisi</i> (Dufour, 1834)					O				Jezberová 2002
				I	I,L,O				SVOBODOVÁ 2010; Sychra 2010
<b>Chrysomelidae</b>									
<i>Donacia obscura</i> Gyllenhal, 1813					L	L	L	L	Sychra 2010
<i>Platamaris sericea</i> (Linnaeus, 1761)							L		Sychra 2010
<b>Total number of species</b>	<b>8</b>	<b>12</b>	<b>22</b>	<b>29</b>	<b>27</b>	<b>20</b>	<b>26</b>	<b>17</b>	
Number of species in lakes	7	7	18	23	22	17	22	14	
Number of species in outlets	5	5	5	11	4	0	2	3	
Number of species in inlets	4	6	6	7	6	5	2	3	
Number of species in inlets and outlets	6	9	9	15	9	5	4	5	

<sup>1)</sup> sub *Gyrinus natator*; <sup>2)</sup> sub *Hydroporus latus*; <sup>3)</sup> sub *Cercyon* sp.

ving substrate and availability of refuges against fish predation (LANDIN 1976b, NILSSON et al. 1994, NILSSON & SÖDERBERG 1996, HEINO 2008, SOLIMINI et al. 2008, ČIAMPOROVÁ-ZAŤOVIČOVÁ et al. 2010, DE MENDOZA & CATALAN 2010). The most species-rich taxocenoses (more than 20 species) were found in the Bohemian Forest lakes with the shallow littoral, which enables development of larger macrophyte beds, especially sedges (Kleiner Arbersee and Laka Lake; 22 species) or at least fragmentary plant beds (Prášílské Lake, 23 species). Slightly lower diversity was recorded in Plešné Lake (18 species), Grosser Arbersee (17 species), and Rachelsee (14 species), where macrophyte beds are developed on more than 10% of the lake perimeter. On the other hand, steep and stony shores of Černé and Čertovo lakes almost without littoral vegetation are rather suitable for some species adapted to predominantly inorganic substrates typical for alpine zones at higher altitudes (HOFFMAN et al. 1996) or lotic habitats. The beetle taxocenoses of these two lakes are markedly species-poorer compared to the other lakes, either with only seven mostly ubiquitous or rhithral species. Except the influence of the absence of littoral macrophytes, beetles diversity can be also negatively affected by the water level fluctuations in Černé Lake due to the small power plant located on its outlet. A negative impact of the water level regulation on littoral invertebrates including aquatic beetles was repeatedly confirmed in several studies of different lakes (e.g., AROVIITA & HÄMÄLÄINEN 2008, BAUMGÄRTNER et al. 2008, BRAUNS et al. 2008). Indeed this negative impact of water level regulation could be far more pronounced some century ago (see Fig. 7 in FRIČ & VÁVRA 1897) in most of the lakes until finishing their use for timber transport.

Also the presence of aquatic mosses in the lake littoral can significantly influence the beetle taxocenoses, especially in the lakes with larger littoral areas composed of peat mosses. In these lakes (Grosser Arbersee and Kleiner Arbersee), typical inhabitants of peat bogs, mainly tytrrophilous beetles were found, e.g., *Hydroporus obscurus*, *Ilybius crassus*, *Enochrus ochropterus*, and *Cyphon punctipennis*. Distribution of some of them exhibits a boreo-alpine pattern in Europe.

#### Species richness of aquatic beetle families

Since the 1890s, when FRIČ & VÁVRA (1897) performed their famous research of two lakes, large flocks of whirligig beetles *Gyrinus substriatus* are known from the water surface of Černé Lake. Pleustonic beetles of the genus *Gyrinus* often congregate in large schools of up to several hundred individuals of more species (ISTOCK 1966, SVENSSON 1985). In September 2010, we have observed these aggregations in several coves of Černé Lake, then we have caught and examined 108 specimens, and all of them were *G. substriatus*. The second species of this genus, *G. marinus*, was found only at Rachelsee, where both species occur.

The family Dytiscidae with 28 recorded species (including larvae of *Acilius* sp.) is the most species-rich group of the aquatic beetle taxocenoses. The most frequent aquatic beetle of the Bohemian Forest lakes (imagines recorded in all eight lakes) is *Hydroporus palustris*, eurytopic small diving beetle, which is very common in all aquatic habitats in the Czech Republic (BOUKAL et al. 2007). This species shows a very abundant population in some lakes (Laka, Prášílské, Čertovo), while populations are relatively scarce in others (Kleiner Arbersee, Černé). This univoltine species has West-Palaeartic distribution; its marked preference for lakes and large bodies of running waters was documented in northern Europe (NILSSON & HOLMEN 1995). Diving beetles *H. memnonius* (found in 5 lakes), *Hydroglyphus geminus* (5 lakes), *Agabus sturmii* (6 lakes), or *Ilybius crassus* (5 lakes) belong to the most frequent species of the lakes.

Eight species from the family Hydrophilidae were found, especially in the well developed vegetated littoral of some lakes. The small water scavenger beetle, *Anacaena lutescens*, very common species of all types of water bodies in the Czech Republic, is particularly frequent

(found in 7 lakes). Chiefly parthenogenetic populations are found in northern and central Europe (HANSEN 1987, BOUKAL et al. 2007). Another eurytopic species, *Hydrobius fuscipes*, is also quite common (found in 5 lakes).

A unique fauna of semi-aquatic beetles inhabit emerged parts of sedges (mainly *Carex rostrata*) of the lake littoral. Yet no special research targeted on these taxa was performed, five species of Scirtidae and Donaciinae (Chrysomelidae) were found (Table 14). Detritivorous aquatic larvae of *Cyphon* spp. have also been found in the littoral of some lakes and occurrence of aquatic larvae of Donaciinae, which are feeding on the submerged sedge parts, is supposed.

#### Permanence and dispersal ability of aquatic beetles

The occurrence of aquatic beetles in the Bohemian Forest lakes can be evaluated from the point of view of permanence and dispersal ability. The species living permanently within the lake water bodies were documented by findings of larvae in different years and seasons (Table 15). Flightless or scarcely flying species certainly belong to this group. Taxa with permanent and abundant occurrence including reproduction in the lakes comprised whirligig beetles (*Gyrinus* spp.), burrowing water beetles (*Noterus* spp.), diving beetles (especially *Agabus* spp., *Dytiscus marginalis*, *Hydroporus* spp., *Ilybius crassus*, *Rhantus exoletus*), and water scavenger beetles (*Anacaena* spp., *Coelostoma orbiculare*, *Helophorus flavipes*, *Hydrobius fuscipes*, *Enochrus* spp.). Especially the lake littoral zones with vegetation and/or organic matter substrates are suitable habitats also for larvae of most of the above genera recently found in the Bohemian Forest lakes (Tables 14, 15). The life cycles of these taxa are semivoltine or flexible (*Agabus bipustulatus*, *A. guttatus*, *Dytiscus marginalis*, *Hydroporus memnonius*) or univoltine with overwintering imagines (*Gyrinus* spp., *Noterus* spp., *Hydroporus palustris*, *H. tristis*, *Hydrobius fuscipes*, *Anacaena lutescens* etc.) as observed in lakes of northern Europe (LANDIN 1976b, HANSEN 1987, NILSSON & HOLMEN 1995). The other permanent inhabitant of the lakes is potamal and silicophilous diving beetle *Nebrioporus assimilis*, which prefers lakes and rivers with sandy bottom and without vegetation, contrary to the above mentioned species. It is mainly distributed in northern and western Europe. In southern parts of the area (southwards to the Alps), the species prefers oligotrophic lakes (NILSSON & HOLMEN 1995). Prášilské Lake and its outlet is the only known recent locality in the Czech Republic (BOUKAL et al. 2012).

Together with aquatic bugs (Heteroptera), aquatic beetles (especially dytiscids) are active fliers and rapid colonisers of various types of water bodies (JEFFRIES 1994, FAIRCHILD et al. 2000, LUNDKVIST et al. 2002). Rapid and agile fliers of the species found are, e.g., *Gyrinus* spp., some species of genera *Hydroporus*, *Agabus* and *Rhantus*, *Dytiscus marginalis*, *Helophorus* spp., and *Anacaena lutescens* (JACKSON 1973, HANSEN 1987, HOLMEN 1987, NILSSON & HOLMEN 1995). In this case, the lakes can serve also as foraging site or temporary habitat. On the other hand, more flightless or scarcely flying species were found: both species of the genus *Noterus*, *Hydroporus obscurus*, *H. tristis*, *H. umbrosus*, *Nebrioporus assimilis*, *Agabus affinis*, and *Anacaena globulus* (JACKSON 1973, HANSEN 1987, HOLMEN 1987, NILSSON & HOLMEN 1995). These species are evidently closely associated with the stable lake littoral environment contrary to the excellent fliers mentioned above.

Some predominantly rheophilic species can reach lakes also from lake inlets or outlets (cf. OERTLI et al. 2008). This is the case of *Deronectes latus*, recorded from Černé and Čertovo lakes (Table 14). This rare flightless diving beetle occurs mostly on gravel or stony substrates in streams and rivers across the Czech Republic (BOUKAL et al. 2007). Similarly also *Agabus guttatus* prefers small running waters and springs and the record of this species from Čertovo Lake could be connected with its frequent occurrence in inlets and outlets of all surveyed lakes (Tables 14, 15).

**Table 15.** Genera (species) of aquatic beetle larvae (Coleoptera) found in the Bohemian Forest lakes in 2002–2011. Species collected in the lakes (see Table 1 for their codes) are in bold; occurrence in individual habitats is distinguished by finding in a lake (L), its inlets (I) and outlet (O); references to unpublished records are not in small caps, i.e., refer to the collector(s) and the year of finding(s).

Family / Species	CN	CT	PL	PR	LA	GA	KA	RA	References
<b>Gyrinidae</b>									
<i>Gyrinus</i> sp.	I								Sychra 2010
<b>Dytiscidae</b>									
<i>Deronectes</i> sp.		L, O	L, O	O					Jezberová 2002
	I	O			O				Sychra 2010
<i>Hydroporus</i> sp.					L				Jezberová 2002
			L						Sychra 2010
<i>Agabus</i> sp.	I, O	I	I, L, O		I, L	L		I	Jezberová 2002
	I, O	I	I, L	I	I, O	I, L	I	I, L, O	SVOBODOVÁ 2010; Sychra 2010,
<i>Ilybius</i> sp.			L	L	L				Sychra 2010; Papáček 2011
<i>Rhantus</i> sp.					L				Jezberová 2002
					L, O				Papáček 2007; SVOBODOVÁ 2010
<i>Actilius</i> sp.				L					Papáček 2011
<i>Dytiscus</i> sp.			L		L	L		L	Sychra 2010; Papáček 2011
<b>Hydrophilidae</b>									
<i>Enochrus</i> sp.					L				Sychra 2010
<b>Scirtidae</b>									
<i>Cyphon</i> sp.		I	L						Sychra 2010
<b>Elmidae</b>									
<i>Limnius perrisi perrisi</i> (Dufour, 1834)					O				SVOBODOVÁ 2010

## Aquatic beetles of lake inlets and outlets

Information on aquatic beetles in inlets and outlets of the Bohemian Forest lakes are scarce, acquired within the first decade of the 21<sup>st</sup> century (Table 14). Altogether 23 taxa have been found in these streams until now. Some of them are typical rheophilic, often flightless or rarely flying species, which frequently occur in small streams and springs in the Czech Republic: *Deronectes latus*, *D. platynotus*, *Hydroporus ferrugineus*, *H. memnonius*, *Oreodytes sanmarkii*, *Agabus biguttatus*, *A. guttatus*, *A. melanarius*, *Anacaena globulus*, *Elmis rioloides*, and *Limnius perrisi* (JACKSON 1973, HANSEN 1987, NILSSON & HOLMEN 1995, BOUKAL et al. 2007). From these inhabitants of streams, 6 species were recorded also in the lakes, although their occurrence there is obviously only temporal and limited to parts of the lake near inlets or outlets. Similarly, 6 species inhabiting lentic habitats were found in marginal parts of lake inlets and outlets.

The most frequent species found in inlets/outlets are dytiscids *Deronectes latus* (6 lakes, more frequent in outlets), *D. platynotus* (5 lakes, more frequent in outlets), *Hydroporus ferrugineus* (4 lakes, only in inlets), *H. palustris* (6 lakes), *Agabus guttatus* (8 lakes, more frequent in outlets), and *A. melanarius* (5 lakes, more frequent in inlets).

Likewise in the lakes, we did not find any response of aquatic beetles to acidification either in inlets or outlets, because the recorded species are mostly acidophilous. Of running water beetles, only the representatives of the genus *Hydraena* were considered less acid-resistant (BRAUKMANN 2001). One specimen of *H. britteni* was found only in the littoral of Laka Lake, which is the least acidified lake in the Bohemian Forest.

This survey of aquatic beetles is the first detailed view on aquatic beetle taxocenoses of the Bohemian Forest lakes. Although it extends our knowledge by several tens of new faunistic records, further research of the lake littoral, as well as other wetland habitats of the Bohemian Forest is necessary.

## Chironomids (Diptera, Chironomidae) – P. Bitušík, J. Peltanová & J. Tátosová

Table 16 shows the complete list of chironomid taxa collected during a period spanned more than one century, from the 1890s to the 2000s. The taxa list is based, in principle, on the presence of pupal exuviae and adults, whose morphological characteristics allow the identification to the species-level. Larvae (seldom pupal exuviae) identified to genus and species group, respectively, were counted only if they represented different taxon. Otherwise they were supposed to belong to the related species/taxa, and they were not numbered and included in the list.

After harmonisation of the data set, the list comprises 113 taxa belonging to five subfamilies. The Orthocladiinae are the most numerous with 54 species/taxa followed by Chironominae (34) and Tanytopodinae (20). In contrast, the Diamesinae and Prodiamesinae are the least represented with only four and one species, respectively.

The majority (75) of the chironomid species/taxa were collected from the lake outlets. However, only 54 species/taxa were found in these habitats exclusively. In the lakes, 48 species/taxa occurred, from that only 29 were captured just in the lakes. The lowest number (17) of chironomid species/taxa was recorded from the lake inlets, eight of them were found in the inlets only.

### Chironomids in the lakes

The most frequently encountered species/taxa recorded mainly in the lakes were *Procladius choreus*, *Corynoneura scutellata*, *Heterotrissocladius grimshawi*, *Heterotrissocladius marcidus*, *Psectrocladius bisetus*, *Chironomus* spp., *Phaenopsectra flavipes*, and *Tanytarsus buchoni*.

The chironomid fauna in the studied lakes is dominated by species/taxa of the subfamily Chironominae (24), 14 of which belong to the Chironomini tribe and 10 to the Tanytarsini tribe. Tanypodinae account for 10 and Orthocladiinae for 13 species/taxa, while Prodiamesinae comprise 1 species. At generic level, a similarity exists in the composition of chironomid fauna between the Bohemian Forest and north European lakes in the boreal zone. The genera *Procladius*, *Chironomus*, and *Tanytarsus* are common chironomid taxa widespread in most of boreal lakes (BRUNDIN 1949, SÆTHER 1979). The *Procladius* pupal exuviae collected from all investigated lakes were identified as *Procladius (Holotanypus) choreus*. One should suppose that larvae found in the outlet of Čertovo Lake (SVOBODOVÁ 2010) and the littoral of Černé Lake (PROCHÁZKOVÁ & BLAŽKA 1999) belong to the same species. EMEIS-SCHWARZ (1985) mentioned the occurrence of *Procladius (Holotanypus) sagittalis* in Grosser Arbersee and Kleiner Arbersee; thus, the presence of more *Procladius* species is quite likely. The larvae of *Chironomus* were recorded in Černé Lake as early as in the 1890s (FRIČ & VÁVRA 1897). Since then, the immature stages were found to be common in all lakes and two outlets. It is reasonable to assume that more than one species are present, but only *Chironomus pseudothummi* found in the outlet of Laka Lake was identified to species level. The occurrence of *Chironomus* cf. *dorsalis* in Rachelsee (SCHÖLL 1989) is unlikely, because the species almost exclusively inhabits temporary habitats, and findings from more permanent environments are rare (FROUZ et al. 2003). *Tanytarsus* belongs to the most species-rich genus in the recorded chironomids. Among the identified species, *Tanytarsus buchoni* is most frequent representative of the Bohemian Forest lakes.

With respect to ecological requirements of the lake chironomids, *Ablabesmyia*, *Psectrocladius*, and *Phaenopsectra* are characteristic for humic and acid lakes (MOSSBERG & NYBERG 1979, WALKER et al. 1985), as well as *Macropelopia adauca*, *Glyptotendipes paripes*, *Pagastiella orophila*, and *Tanytarsus buchoni* prefer dystrophic conditions (DOWLING & MURRAY 1981, DOGHERTY & MORGAN 1991, EKREM 2004). Among those, *Psectrocladius barbatipes*, *P. bisetus*, *P. oligosetus*, *Phaenopsectra* Pe f. Bala, and *Tanytarsus* cf. *smolandicus* are considered as cold stenothermic. Furthermore, the *Heterotrissocladius*, *Parakiefferiella*, *Phaenopsectra*, and *Sergentia* species are known from deeper, well-oxygenated lakes in Europe (e.g., HOFFMANN 1988, MOUSAVI 2002).

The previous study (BITUŠÍK & SVITOK 2006) showed that differences in taxonomic composition among the Bohemian Forest lakes can be explained significantly by different altitude and alkalinity of the lakes. Moreover, the ordination analysis revealed the great importance of geographical gradient (from west to east), which could include geology of the catchments, distances between the lakes, and historical human influence on the lakes, as well.

#### Chironomids of inlets and outlets

Due to the intensive sampling at the outlets of Laka and Čertovo lakes (SVOBODOVÁ 2010), the chironomid fauna is more representative for the outlets than for the lake inlets. The stream fauna is composed largely of rheobiotic/rheophilic taxa (e.g., *Apsectrotanypus*, *Conchapelopia*, *Nilotanypus*, *Diamesa*, *Pseudodiamesa*, *Brillia*, *Cricotopus*, *Eukiefferiella*, *Heleniella*, *Krenosmittia*, *Orthocladius*, *Paratrachocladius*, *Rheocricotopus*, *Tvetenia*, *Polypedilum*). The taxocenoses consist regularly of some lentic taxa that larvae and pupal exuviae were washed up from the lakes (*Procladius*, *Psectrocladius*, *Chironomus*, *Glyptotendipes*, *Endochironomus*, *Phaenopsectra*, *Sergentia*, *Paratanytarsus*). Most species of *Psectrocladius* (s. str.) are widely distributed in stagnant waters ranging from small, shallow bodies to reservoirs and lakes (LANGTON 1980). The finding of *Psectrocladius bisetus* in the inlet of Prášilské Lake is an evidence that the species can develop in flowing waters.

**Table 16.** Species/taxa of non-biting midges (Diptera, Chironomidae) found in the Bohemian Forest lakes in 1897–2010. Species collected in the lakes (see Table 1 for their codes) are in bold; occurrence in individual habitats is distinguished to findings in a lake (L), its inlets (I) and outlet (O); findings of pupal exuvia (pe) or imagines (im) enable a determination to the species level; possible references to unpublished records are not in small caps, i.e., refer to the collector(s) and the year of finding(s).

Subfamily, tribe / Species	CN	CT	PL	PR	LA	GA	KA	RA	References
Tanypodinae, Procladini									
<i>Procladius (Holotanypus) choreus</i> (Meigen, 1804)	Lpe	Lpe, Ope	Lpe, Ope	Lpe, Ope	Lpe	Lpe	Lpe	Lpe	BITUŠÍK & SVITOK 2006; BITUŠÍK 2010; SVOBODOVÁ 2010; PROCHÁZKOVÁ & BLAŽKA 1999
<i>Procladius (Holotanypus) sagittalis</i> (Kieffer, 1909)						Lpe, Lim	Lim		EMEIS-SCHWARZ 1985
Tanypodinae, Macropelopiini									
<i>Aspexitrotanypus trifascipennis</i> (Zetterstedt, 1838)					O				SVOBODOVÁ 2010
<i>Macropelopia adaucta</i> Kieffer, 1916	Lpe	Lpe				Lpe	Lpe, Lim		EMEIS-SCHWARZ 1985; BITUŠÍK & SVITOK 2006; BITUŠÍK 2010
<i>Macropelopia nebulosa</i> (Meigen, 1804)								L	SCHÖLL 1989; Matěna 1999
<i>Macropelopia notata</i> (Meigen, 1818)				L					Matěna 1999
Tanypodinae, Natarsiini									
<i>Natarsia punctata</i> (Fabricius, 1805)			O						Matěna 1999
Tanypodinae, Pentaneurini									
<i>Ablabesmyia monilis</i> (Linnaeus, 1758)	Lpe	Lpe				Lpe, Lim	Lpe, Lim	Lpe	EMEIS-SCHWARZ 1985; BITUŠÍK & SVITOK 2006
<i>Ablabesmyia phatta</i> (Egger, 1863)						Lpe			BITUŠÍK & SVITOK 2006
<i>Arctopelopia</i> cf. <i>griseipennis</i> (van der Wulp, 1859)					Lpe				BITUŠÍK 2010
<i>Conchapelopia melanos</i> (Meigen, 1818)			O	Ope					Matěna 1999; BITUŠÍK 2010
<i>Conchapelopia</i> cf. <i>intermedia</i> Fittkau, 1962				O					Matěna 1999
<i>Nilotanypus dubius</i> (Meigen, 1804)					O				SVOBODOVÁ 2010
<i>Rheopelopia</i> sp.					O				Matěna 1999
<i>Thienemannimyia carneae</i> (Fabricius, 1805)			O						Matěna 1999
<i>Trissopelopia</i> sp.				O	O				Matěna 1999; SVOBODOVÁ 2010
<i>Zavrelimyia</i> cf. <i>punctatissima</i> (Goetghebuer, 1934)			Lpe						BITUŠÍK & SVITOK 2006
<i>Zavrelimyia melanura</i> (Meigen, 1804) / <i>barbatipes</i> (Kieffer, 1911)		Lpe	Lpe	Lpe	Lpe				BITUŠÍK & SVITOK 2006; BITUŠÍK 2010
<i>Zavrelimyia</i> cf. <i>nubila</i> (Meigen, 1830)	Ipe	Ipe							BITUŠÍK 2010
<i>Zavrelimyia</i> sp.			Lpe						BITUŠÍK & SVITOK 2006

Table 16. Continued

Subfamily, tribe / Species	CN	CT	PL	PR	LA	GA	KA	RA	References
<b>Diamesinae, Diamesini</b>									
<i>Diamesa tonsa</i> group					O				Svobodová 2010
<i>Diamesa</i> sp.			O	O					Matěna 1999
<i>Pothisia longimanus</i> Kieffer, 1922		O			O				Svobodová 2010
<i>Pseudodiamesa branicicki</i> (Nowicki, 1873)		O		O	O				Matěna 1999; Svobodová 2010
<b>Prodiamesinae</b>									
<i>Prodiamesa olivacea</i> (Meigen, 1818)	L	O	O	Lpe, L, O	L,O				Matěna 1999; Btůšek & Svítok 2006; Svobodová 2010
<b>Orthocladinae</b>									
<i>Brillia bifida</i> (Kieffer, 1909)		O			O				Svobodová 2010
<i>Bryophanocladius</i> cf. <i>subvernalis</i> (Edwards, 1929)		Ope							Btůšek 2010
<i>Cardiocladius capucinus</i> (Zetterstedt, 1850)				O					Matěna 1999
<i>Chaetocladius dissipatus</i> (Edwards, 1929)		Lpe							Btůšek 2006
<i>Corynoneura lobata</i> Edwards, 1924		Ipe, O	Ipe	Lpe	Lpe	Lpe	Lpe		Btůšek 2011; Svobodová 2010
<i>Corynoneura scutellata</i> Winnertz, 1846	Lpe		Ipe, Lpe	Lpe					Btůšek 2006; Btůšek & Svítok 2006; Btůšek 2010
<i>Corynoneura</i> cf. <i>coronata</i> Edwards, 1924		O							Svobodová 2010
<i>Cricotopus (Cricotopus) pulchripes</i> Verrall, 1912				Ope					Btůšek 2011
<i>Cricotopus (Cricotopus)</i> cf. <i>magus</i> Hirvenoja, 1973						Lpe			Btůšek & Svítok 2006
<i>Cricotopus (Cricotopus)</i> cf. <i>patens</i> Hirvenoja 1973		O			O				Svobodová 2010
<i>Eukiefferiella breviculcar</i> (Kieffer, 1911)		Ipe			O				Btůšek 2010; Svobodová 2010
<i>Eukiefferiella claripennis</i> (Lundbeck, 1898)					O				Svobodová 2010
<i>Eukiefferiella devonica</i> (Edwards, 1929)					O				Svobodová 2010
<i>Eukiefferiella fuldensis</i> Lehmann, 1972/ <i>coerulescens</i> (Kieffer, 1926)		O			O				Svobodová 2010
<i>Eukiefferiella</i> cf. <i>minor</i> (Edwards, 1929)					O				Svobodová 2010
<i>Eukiefferiella pseudomontana</i> Goetghebuer, 1935					O				Svobodová 2010
<i>Eukiefferiella</i> cf. <i>tirolensis</i> Goetghebuer, 1938				Ipe					Btůšek 2010
<i>Eukiefferiella brehmi</i> group					O				Svobodová 2010
<i>Eukiefferiella similis</i> group					O				Svobodová 2010
<i>Georthocladius</i> sp.		Ipe							Btůšek 2010
<i>Heleniella</i> sp.					O				Svobodová 2010
<i>Heteronyctarus</i> cf. <i>apicalis</i> (Kieffer, 1921)		O							Svobodová 2010
<i>Heteronyctarus</i> cf. <i>grimshawi</i> (Edwards, 1929)	Lpe	Lpe	Ope		Lpe,O	Lpe	Lpe	Lpe	Btůšek & Svítok 2006; Btůšek 2010; Svobodová 2010

Table 16. Continued

Subfamily, tribe / Species	CN	CT	PL	PR	LA	GA	KA	RA	References
<i>Heterotrioxocladus marcidus</i> (Walker, 1856)	Ipe, Lpe, L	Ipe, Lpe, Ope, O	Ipe, Lpe	Lpe, L	O	Lpe, Lim	Lpe	L	EMEIS-SCHWARZ 1985; SCHÖLL 1989; PROCHÁZKOVÁ & BLAŽKA 1999; Matěna 1999; BITUŠÍK & SVITOK 2006; SVOBODOVÁ 2010; BITUŠÍK 2010 BITUŠÍK 2011
<i>Krenosmittia borealpina</i> (Goetghebuer, 1944)	Ipe			Ipe	O				SVOBODOVÁ 2010
<i>Krenosmittia</i> sp.		O							BITUŠÍK 2011
<i>Linnophyes gurgicola</i> (Edwards, 1929)		Ipe, Ope	Ipe, Lpe						SVOBODOVÁ 2010
<i>Merricnemus</i> sp.					O				SVOBODOVÁ 2010
<i>Nanocladius parvulus</i> group					O				SVOBODOVÁ 2010
<i>Orthocladus</i> ( <i>Symptostocladus</i> ) <i>lignicola</i> (Kieffer, 1914)		O							SVOBODOVÁ 2010
<i>Orthocladus</i> sp.					O				SVOBODOVÁ 2010
<i>Parachaetocladus</i> sp.		O							SVOBODOVÁ 2010
<i>Parakiefferiella bathophila</i> (Kieffer, 1912)	Ipe, Lpe		Lpe, Ope		Lpe				BITUŠÍK & SVITOK 2006; BITUŠÍK 2011
<i>Paralinnophyes</i> sp.					O				SVOBODOVÁ 2010
<i>Paraphaenocladus pseudirritus</i> Srenzke, 1950		Ipe							BITUŠÍK 2011
<i>Paratrichocladius rufiventris</i> (Meigen, 1830)					O				SVOBODOVÁ 2010
<i>Paratrichocladius skirwithensis</i> (Edwards, 1929)					O				SVOBODOVÁ 2010
<i>Psectrocladius</i> ( <i>Mesopsectrocladius</i> ) <i>barbatipes</i> Kieffer, 1923					Lpe				BITUŠÍK & SVITOK 2006; BITUŠÍK 2010
<i>Psectrocladius</i> ( <i>Psectrocladius</i> ) <i>bisetus</i> Goetghebuer, 1942	Lpe	Lpe		Ipe, Ope	Lpe	Lpe	Lpe		BITUŠÍK 2006; BITUŠÍK & SVITOK 2006; Bitušík 2010
<i>Psectrocladius</i> ( <i>Psectrocladius</i> ) <i>oligotenus</i> Wülker, 1956			Lpe		Lpe	Lpe			BITUŠÍK 2006; BITUŠÍK & SVITOK 2006; Bitušík 2010
<i>Psectrocladius</i> ( <i>Psectrocladius</i> ) <i>psilopterus</i> (Kieffer, 1906)		O		Lpe	O	Lpe	Lpe		BITUŠÍK & SVITOK 2006; BITUŠÍK 2010; SVOBODOVÁ 2010
<i>Psectrocladius</i> ( <i>Psectrocladius</i> ) <i>sordidellus</i> Zetterstedt, 1838			Lpe	Lpe		Lim	Lim	Lpe	EMEIS-SCHWARZ 1985; BITUŠÍK & SVITOK 2006; SVOBODOVÁ 2010
<i>Psectrocladius</i> ( <i>Psectrocladius</i> ) <i>PeA</i> Langton, 1991/ <i>oxyura</i> Langton, 1985			Lpe, Ope						Bitušík 2010

Table 16. Continued

Subfamily, tribe / Species	CN	CT	PL	PR	LA	GA	KA	RA	References
<i>Pseudorthocladius filiformis</i> (Kieffer, 1908)		lpe, Ope		lpe					BITUŠÍK 2011
<i>Pseudorthocladius</i> sp.		lpe							BITUŠÍK 2010
<i>Pseudosmittia</i> sp.		O			O				SVOBODOVÁ 2010
<i>Rheocricotopus (Rheocricotopus) effusus</i> (Walker, 1856)					O				SVOBODOVÁ 2010
<i>Rheocricotopus (Rheocricotopus) fuscipes</i> (Kieffer, 1909)					O				SVOBODOVÁ 2010
<i>Smittia</i> sp.		O							SVOBODOVÁ 2010
<i>Thienemanniella</i> sp.					O				SVOBODOVÁ 2010
<i>Thienemanniella</i> cf. <i>parvita</i> Schlee, 1968		O			O				SVOBODOVÁ 2010
<i>Thienemanniella clavicornis</i> group					O				SVOBODOVÁ 2010
<i>Thienemanniella</i> sp.					O				SVOBODOVÁ 2010
<i>Tvetenia calvescens</i> (Edwards, 1929)		Ope,O		Ope, O	O				Matěna 1999; BITUŠÍK 2011; SVOBODOVÁ 2010
<b>Chironominae, Chironomini</b>									
<b>Chironomus</b> spp.									
<i>Chironomus pseudothummi</i> Strenzke, 1959	L	Lpe, L, Ope, O	Lpe	Lpe, L	Lpe, L, O	Lpe, Lim	Lpe, Lim	L	FRÍČ & VÁVRA 1897; EMEIS-SCHWARZ 1985; SCHÖLL 1989; Matěna 1999; BITUŠÍK & SVITOK 2006; SVOBODOVÁ 2010; BITUŠÍK 2010
<i>Cryptochironomus</i> cf. <i>defectus</i> (Kieffer 1913)	L				O				Matěna 1999
<i>Dicrotendipes</i> sp.		O							Matěna 1999
<b>Endochironomus albipennis</b> (Meigen, 1830)		Lpe, O			O		Lpe		SVOBODOVÁ 2010
<b>Glyptotendipes (Glyptotendipes) cf. cauliginellus</b> (Kieffer, 1913)	L								BITUŠÍK & SVITOK 2006; SVOBODOVÁ 2010; BITUŠÍK 2010
<b>Glyptotendipes (Glyptotendipes) paripes</b> (Edwards, 1929)		Lpe, O		Lpe					Matěna 1999
<b>Glyptotendipes</b> sp.	L			L					BITUŠÍK & SVITOK 2006; BITUŠÍK 2010; SVOBODOVÁ 2010
<i>Kiefferulus tenuipaliformis</i> (Goetghebuer, 1921)	Lpe								Matěna 1999
<b>Microtendipes pedicellus</b> group	L			L					BITUŠÍK 2010
<i>Pagasiella orophila</i> (Edwards, 1929)							Lpe		PROCHÁZKOVÁ & BLAŽKA 1999; Matěna 1999
<b>Phaenopsectra flavipes</b> (Meigen, 1818)	Lpe	Lpe	Lpe, Ope	Lpe, Ope	Lpe	Lpe	Lpe		EMEIS-SCHWARZ 1985
									EMEIS-SCHWARZ 1985; BITUŠÍK & SVITOK 2006; BITUŠÍK 2010

Table 16. Continued

Subfamily, tribe / Species	CN	CT	PL	PR	LA	GA	KA	RA	References
<i>Phaenopsectra</i> cf. <i>punctipes</i> (Wiedemann, 1817)		Lpe							Bitušik 2010
<i>Phaenopsectra</i> Pe f. Bala Langton, 1991							Lpe		Bitušik & Svítok 2006
<i>Polypedium (Polypedium) albicorne</i> (Meigen, 1838)			Ope		O				Bitušik 2010; SVOBODOVÁ 2010
<i>Polypedium (Polypedium) laetum</i> (Meigen, 1818)					O				SVOBODOVÁ 2010
<i>Polypedium (Polypedium) cf. pedestre</i> (Meigen, 1830)				O	O				Matěna 1999; SVOBODOVÁ 2010
<i>Polypedium (Uresipedium) cf. convictum</i> (Walker, 1856)					O				SVOBODOVÁ 2010
<i>Polypedium (Tripodura) scalaenum</i> group					O				SVOBODOVÁ 2010
<i>Sergenia</i> cf. <i>coracina</i> Zetterstedt, 1850		Lpe, Ope							Bitušik 2010
<i>Stictochironomus</i> sp.				O					Matěna 1999
<i>Synendotendipes</i> sp.						Lpe			Bitušik & Svítok 2006
<b>Chronominae</b> , Tanytarsini									
<i>Micropsectra atrofasciata</i> (Kieffer, 1911)		Ipe							Bitušik 2011
<i>Micropsectra atrofasciata</i> agg.	Ipe	Ipe		Ipe, Ope				L	SCHÖLL 1989; Bitušik 2010
<i>Micropsectra fusca</i> (Meigen, 1804)			Ipe					L	SCHÖLL 1989; Bitušik 2011
<i>Paratanytarsus penicillatus</i> (Goetghebuer, 1928)					Lpe				Bitušik 2010; SVOBODOVÁ 2010
<i>Stempellinella brevis</i> (Edwards, 1929)	L	O			Lpe,O				PROCHÁZKOVÁ & BLÁŽKA 1999; Bitušik 2010; SVOBODOVÁ 2010
<i>Tanytarsus buchonius</i> Reiss et Fittkau, 1971	Lpe	Lpe, Ope	Lpe, Ope	Lpe, Ope	Lpe	Lpe, Lim	Lpe	Lpe	EMEIS-SCHWARZ 1985; Bitušik 2006; Bitušik & Svítok 2006; Bitušik 2010
<i>Tanytarsus debilis</i> (Meigen, 1830)/ Pe4c Langton, 1991		Ope		Lpe					Bitušik 2010
<i>Tanytarsus curticornis</i> Kieffer, 1911									Bitušik 2011
<i>Tanytarsus signatus</i> (van der Wulp, 1858)	Lpe	Lpe					Lpe	Lpe	Bitušik 2006; Bitušik & Svítok 2006; Bitušik 2010
<i>Tanytarsus</i> cf. <i>smolandicus</i> Brundin, 1947							Lpe	Lpe	Bitušik & Svítok 2006
<i>Tanytarsus lestajeti</i> agg.									Bitušik & Svítok 2006
<i>Tanytarsus pallidicornis</i> (Walker, 1856)					Lpe				Bitušik & Svítok 2006
<b>Total number of species</b>	<b>22</b>	<b>46</b>	<b>24</b>	<b>30</b>	<b>57</b>	<b>18</b>	<b>18</b>	<b>11</b>	SCHÖLL 1989
Number of species in lakes	19	16	14	15	16	18	18	11	
Number of species in outlets	0	30	13	16	45	0	0	0	
Number of species in inlets	5	11	5	5	0	0	0	0	
Number of species in inlets and outlets	5	37	18	19	45	0	0	0	

In addition, the streams host a number of species characteristic for semi-terrestrial and/or madicolous habitats (ARMITAGE et al. 1995: *Bryophaenocladus* cf. *subvernalis*, *Georthocladus* sp., *Metriocnemus* sp., *Limnophyes gurgicola*, *Parachaetocladus*, *Paraphaenocladus pseudirritus*, *Pseudorthocladus filiformis* or *Smittia* sp.).

Past studies of chironomids in the Bohemian Forest lakes have not been half as comprehensive as they should have been corresponding to their importance. They contribute a lot in terms of density, relative abundance, as well as taxa numbers to macroinvertebrate assemblages. More recent studies of the lakes, their inlets and outlets revealed 13 species recorded for the first time in the Czech Republic (BITUŠÍK & KUBOVČÍK 2000, BITUŠÍK 2011) but this number is far from complete. Further investigations will very likely result in findings of more new species to the Czech fauna.

#### Historical and palaeolimnological records

Compared to mayflies and stoneflies (SOLDÁN et al. 1998, 1999, this study), historical data on chironomids are too scanty to reconstruct changes caused by strong acidification during the last century. The chironomid data before the 1950s, which could be considered as “reference data” prior to the acidification onset of the Bohemian Forest lakes, are not available so that our data set from the 1990s and 2000s reflects rather the processes of biological recovery than the changes connected with acidification. An indirect method providing valuable information on the chironomid composition during the whole lake ontogeny is analysis of chironomid subfossil remains from lake sediments. Three palaeolimnological studies used subfossil chironomids to trace the environmental characteristics of the Bohemian Forest lakes in the past. Two of them were aimed primarily to document an evidence of the acidification history. All studies showed in general a consistent picture: a pauperisation of the lake chironomid fauna in the last century.

BITUŠÍK & KUBOVČÍK (2000) analysed chironomid remains from short (19.5 cm) sediment cores taken from Černé and Prášilské lakes in 1991. The study showed that the acidification process was connected with a decline in sub-fossil remains and with the disappearance of certain taxa (*Dicrotendipes*, *Microtendipes pedellus* group, *Polypedilum*, *Paratanytarsus*, *Zavelia*) in the most recent sediment layers. These species have not been found in the recent samples from the lakes. It is reasonable to suppose negative influence of some other factors connected with low pH (e.g., high concentrations of total reactive Al and trace metals; FOTT et al. 1994, VESELÝ et al. 1998b), because some of these taxa are reported from acid conditions (*Dicrotendipes*, *Microtendipes*, *Pagastiella*; WIEDERHOLM & ERIKSSON 1977, SCHNELL & WILLASSEN 1996). In general, chironomids did not reflect the effects of acidification in the investigated lakes in such a dramatic way as Ephemeroptera and Plecoptera (VRBA et al. 2003a, this study). Chironomid larvae, they live burrowing in the sediment where microbial processes on the water-sediment interface can effectively mitigate harmful water chemistry (i.e. low pH, Al toxicity). It also seems that the chironomid taxocenoses in acidified lakes respond rather to the changes in quantity and quality of food supply than to the direct physiological effect of low pH. Insufficient food supply could be either connected with lower availability of phosphorus in the lake due to its precipitation by aluminium (VRBA et al. 2006) or with changes in fish and invertebrate assemblages (BRODIN 1990, HYNYNEN & MERILÄINEN 2005).

The analysis of the sediment record from Kleiner Arbersee (EMEIS-SCHWARZ & KOHMANN 1984) revealed taxonomic-rich chironomid assemblages consisting of 42 taxa. Taxonomic composition with prevalence of Tanytarsini, *Heterotrissocladus*, and *Psectrocladius* was indicative for oligotrophic and oligo-humic conditions. The most notable shift in chironomids was observed at the end of the studied period: a decrease in total number of taxa, a

disappearance of Tanytarsini and an increase in *Chironomus* and *Tribelos*. Even if the shift well corresponded with an acidification event, it could also indicate elevated nutrient conditions. In addition to acidification, the subfossil chironomids indicated other human-induced changes in the last ~200 years, particularly fluctuations in the water level.

Unique palaeolimnological records are available from the 5.4 m long sediment core of Plešné Lake covering a period of 14.7 ka cal BP (TĀTOSOVÁ et al. 2006). In this whole Holocene sediment profile, 47 taxa were identified. In the early stages of the lake ontogeny, the cold stenothermic taxa dominated (*Micropsectra radialis*-type, *Pseudodiamesa nivosa*-type, *Diamesa* sp., *Heterotrissocladius grimshawi*-type, *Paracladius* sp.). Later, *Heterotrissocladius marcidus*-type and *Corynoneura scutellata*-type became dominant at the beginning of the Holocene, accompanied by such genera as *Microtendipes*, *Zavrelimyia*, *Parakiefferiella*, *Dicotendipes* and *Cricotopus*. In the middle of the Holocene, characterised by optimal climate conditions, the dominance of *H. marcidus*-type and *C. scutellata*-type was reduced and the chironomid taxocenoses became more diverse as other taxa appeared (*Phaenopsectra*, *Limnophyes/Paralimnophyes*, *Cladotanytarsus*, *Ablabesmyia*, *Psectrocladius psilopterus*-type). The relatively stable and diverse chironomid taxocenose was interrupted by an event in 1540–1771 AD, when most of the taxa totally vanished and the chironomid fauna was composed by only *Zavrelimyia* sp. and *Procladius* sp. alternately, accompanied by *Tanytarsus* sp. This event is in agreement with the dating of the Little Ice Age and could be the result of low oxygen concentrations at the lake bottom caused by longer winter ice cover (LINDEGAARD 1995, HEIRI & LOTTER 2003). However, these sediment layers also coincide with an episode of very low chironomid abundances, which makes the fossil chironomid record less reliable.

The sub-sampling by 3-cm layer was too rough for detailed analysis of an acidification effect on chironomid taxocenoses, nevertheless, the first three layers (0–9 cm) corresponding to the period from the beginning of the 20<sup>th</sup> century to 1990 (when the sediment core was collected) can be used for a tentative interpretation. The most recent sediment (1956–1990 AD) was very species-poor. Only five taxa in very low densities were found as compared to the previous two layers (3–9 cm), in either of which 13 taxa occurred. Most of the taxa present in the foregoing layers disappeared (*Zavrelimyia* sp., *Dicotendipes nervosus*-type, *Microtendipes pedellus*-type, *Phaenopsectra flavipes*-type, *Cladotanytarsus mancus*-type 2, *Limnophyes* sp., *Psectrocladius psilopterus*-type, *Cricotopus intersectus*-type, *Parakiefferiella bathophila*-type, *Heterotrissocladius marcidus*-type) and the chironomid fauna was formed only by *Procladius* sp., *Chironomus anthracinus*-type, *Cladotanytarsus mancus* type 1, *Tanytarsus pallidicornis*-type, and *Corynoneura arctica*-type. Considering the acidophilic or acidotolerant ecology known for the genera *Heterotrissocladius*, *Psectrocladius*, *Cladotanytarsus*, and also *Phaenopsectra* (BROOKS et al. 2007), the species reduction during the second half of the last century may be a result from other factors than acid stress.

### **Other families of flies (Diptera) – T. Soldán & J. Bojková**

Species richness of Diptera taxocenoses

The Diptera taxocenoses (excluding Chironomidae) represent a considerably heterogeneous group, the study of which seems to be most difficult in comparison with other orders occurring in the Bohemian Forest lakes. There are two principal causes tending to an apparent underestimation in evaluation of true species richness. It is necessary to study imagines of flies, because an insufficient knowledge of larvae does not allow for a proper determination of larvae (only 654 species of 1220 aquatic Diptera living the Czech Republic have been described in the larval stage; cf. ROZKOŠNÝ & VAŇHARA 2004), on the one hand, and use

specialised collecting techniques in some groups and habitats (aquatic–terrestrial ecotone), on the other hand. Although we did our best in trying to determine all taxa at the lowest level as possible, we did not avoid letting some of them at the generic and even family level, because no attention has been devoted to collecting of imagines to precise determination of larvae.

Of the 29 families (excluding Chironomidae), there are 1220 species with larvae inhabiting purely aquatic or semiaquatic environment (ROZKOŠNÝ & VAŇHARA 2004). A total of 17 families (about 59%) and 37 taxa (9 determined at the species level, 24 at the generic level and 4 at the higher levels) have been found in the Bohemian Forest lakes (Table 17). Twelve species/taxa were found in lakes and 27 species/taxa in their inlets/outlets. Some further families certainly were observed in the imaginal stage near the lakes (e.g., Dolichopodidae or Sciomyzidae) but these taxa were not detected in the larval stage.

#### Taxa richness of Diptera families

The family Limoniidae (152 of 271 craneflies are aquatic in the Czech Republic; data presented in all families are based on list by ROZKOŠNÝ & VAŇHARA 2004) showed the highest taxa richness (8 taxa), although the only one species, *Pilaria discicollis* occurring in Plešné Lake and Rachelsee, was determined to the species level. Besides this species and *Hexatoma* sp. from Rachelsee, all taxa have been found in the inlets/outlets only. Larvae of the genus *Eloeophila* were most frequent (Table 17).

The family Pediciidae (within the Czech Republic, 30 of 34 species are aquatic), although represented only by two taxa, namely genera *Dicranota* and *Pedicia* (species cannot be determined due to insufficient knowledge of larval diagnostic characters), belongs to the most frequent taxa within the lakes also by abundance (SENOO 2009, SVOBODOVÁ 2010). They were not collected in the lakes but inhabited nearly all inlets and outlets (Table 17).

Representatives of the family Tipulidae (within the Czech Republic, 48 of 123 species are aquatic) were restricted solely to the lake inlets where they are not abundant. Specimens of *Tipula* (*Savtshenkia*) have been collected usually as a single larva in each inlet. SVOBODOVÁ (2010) determined *Tipula* (*Emodotipula*) *obscuriventris* (as *Tipula saginata*) and *Tipula* (*Savtshenkia*) cf. *cheethami* collected downstream (at the distance of 1.7–2.8 km) in the outlet of Laka Lake.

Larvae of the family Simuliidae (all 42 species aquatic) have been collected in inlets of nearly all Bohemian Forest lakes and in all outlets (Table 17). We determined two species, *Simulium* (*Simulium*) *argyreatum* and *S. (Simulium) ornatum*, in several lakes (cf. Table 17). Larvae of an unidentified species of the genus *Prosimulium* were collected mostly in inlets of Černé and Čertovo lakes and inlets/outlet of Plešné Lake (SENOO 2009), and in the outlet of Rachelsee (JEZBEROVÁ, unpubl.).

The larvae of *S. ornatum* were collected only incidentally (they prefer running waters) in the lakes near the mouth of inlets or in the beginning of an outlet. The larvae are relatively abundant (but never eudominant) in inlets, although they can reach considerable abundance in outlets. For instance, SENOO (2009) found *Simulium* sp. and *Prosimulium* sp. to reach 11% and 5% of all collected individuals, respectively, in the outlet of Prášilské Lake. Mass aggregations are due to feeding strategy of the Simuliidae larvae. As filtrators, they meet sufficient amount of drifting seston from the lake. This phenomenon is obvious in Laka and Plešné lakes, but very pronounced in Prášilské Lake. In several meters long, artificial concrete section of outlet below the lake, larvae of *S. argyreatum* currently reach densities that might be roughly estimated up to >10 000 ind.m<sup>-2</sup>, as any place of the bottom is densely covered with larvae. Abundance of larvae rapidly decreases downstream and larvae occur rather individually at distance of about 100 m from beginning of the outlet; their mass aggregations

**Table 17.** Species/taxa of Diptera except Chironomidae found in the Bohemian Forest lakes in 1999–2010. Species collected in the lakes (see Table 1 for their codes) are in bold; occurrence in individual habitats is distinguished to findings in a lake (L), its inlets (I) and outlet (O); references to unpublished records are not in small caps, i.e., refer to the collector(s) and the year of finding(s).

<b>Family /Species</b>	<b>CN</b>	<b>CT</b>	<b>PL</b>	<b>PR</b>	<b>LA</b>	<b>GA</b>	<b>KA</b>	<b>RA</b>	<b>References</b>
Suborder <b>Nematocera</b>									
<b>Limoniidae</b>									
<i>Eloephila</i> sp.				I	I,O				Soldán 2010
<i>Euphytidorea cf. meigenii</i> (Verrall, 1887)	O			I	I,O	I	I		SENOO 2009; SVOBODOVÁ 2010
<i>Euphytidorea / Phylidorea</i> sp.		I,O			I				SENOO 2009
<b>Hexatoma</b> sp.								L	Soldán 2010
<i>Limnophila</i> sp.		O							SVOBODOVÁ 2010
<i>Neolimnomyia (Brachylimnophila) cf. nemoralis</i> (Meigen, 1818)			I						SENOO 2009
<b>Pilaria discicollis</b> (Meigen, 1818)		L						L	Soldán 2010
<i>Ormosia</i> sp.			I						SENOO 2009
<b>Peditidae</b>									
<i>Dicranota</i> sp.		I		I	I,O	I			Soldán 2010
<i>Pedicia</i> sp.	I,O	I,O	I	I,O	I,O	I	I	I	Soldán 2009; SVOBODOVÁ 2010
	I	I	I	I	I	I	I,O	I	Soldán 2010
	I	I,O	I	I,O	I,O	I	I		SENOO 2009; SVOBODOVÁ 2010
<b>Psychodidae</b>									
<i>Psychoda cf. phalaenoides</i> (Linnaeus, 1758)	O								Soldán 1999
<b>Tipulidae</b>									
<i>Dolichopeza albipes</i> (Ström, 1768)	I	I		I	I				SENOO 2009
<i>Tipula (Savitschenkia)</i> sp.		I	I	I					Jezberová 2002
	I,O	I	I	I	I				SENOO 2009
<b>Simuliidae</b>									
<i>Prosimulium</i> sp.		I						O	Jezberová 2002, 2003
	I	I	I,O						SENOO 2009
<i>Simulium (Simulium) argyreatum</i> Meigen, 1838		O	O	O	O	I		O	Soldán 2010
<b>Simulium (Simulium) ornatum</b> Meigen, 1818		O		L,I	O		O	I,O	Soldán 2010
<i>Simulium</i> sp.	I,O	O	SENOO 2009						
<b>Culicidae</b>									
<i>Aedes (Aedimorphus) vexans</i> Meigen, 1830							I	I	Soldán 1999, 2002
<i>Anopheles (Anopheles)</i> sp.							I		Jezberová 2003
<b>Ochlerotatus</b> sp.					I,I	I			Soldán 2010
<b>Dixidae</b>									
<i>Dixa</i> sp.			O	I,O				L	Jezberová 2002, 2003

Table 17. Continued

Family / Species	CN	CT	PL	PR	LA	GA	KA	RA	References
<i>Dicella amphibia</i> (De Geer, 1776)			L						Soldán 2010
<b>Ceratopogonidae</b>									
<i>Atrichopogon</i> sp.		I	I	I					SENOO 2009
Ceratopogonidae gen. sp.		I,O	I,O	I	I		L		Soldán 2010
	I,O			O	O		I		SENOO 2009; SVOBODOVÁ 2010
	L		L		L		L	L	UNGERMANOVA 2009
Ceratopogonidae, Dasyheleinae gen. sp.			L		L				Soldán 1999
<b>Chaoboridae</b>									
<i>Chaoborus</i> ( <i>Chaoborus</i> ) <i>obscuripes</i> (Van Der Wulp, 1859)					L				Soldán 2010
<i>Chaoborus</i> sp.					L	L	L		UNGERMANOVA 2009
<b>Blephariceridae</b>									
<i>Liponeura</i> sp.			O		O				Soldán 1999, 2002
<b>Cecidomyiidae</b>									
Cecidomyiidae gen. sp.		O							SVOBODOVÁ 2010
Suborder <b>Brachycera</b>									
<b>Rhagionidae</b>									
<i>Rhagio</i> sp.			I						SENOO 2009
<b>Athericidae</b>									
<i>Ibisia marginata</i> (Fabricius, 1781)								O	Jezberová 2003
<b>Tabanidae</b>									
<i>Haematopota</i> cf. <i>pluvialis</i> (Linnaeus, 1758)							L		Jezberová 2003
<i>Hybomitra</i> sp.							L	L	Soldán 2010
<i>Tabanus</i> sp.						L			Soldán 2010
<b>Empididae</b>									
<i>Chelifera</i> sp.	I	I	I	I	I,O				SENOO 2009; SVOBODOVÁ 2010
<i>Clinocera</i> sp.	I				O		I		SENOO 2009
<i>Wiedemannia</i> sp.	I,O	I	I	I	I		I		SENOO 2009
<b>Syrphidae</b>									
<i>Eristalis</i> sp.						O			Jezberová 2003
<b>Muscidae</b>									
<i>Limnophora</i> sp.			O						SENOO 2009
<b>Total number of species/taxa</b>	<b>12</b>	<b>15</b>	<b>19</b>	<b>13</b>	<b>17</b>	<b>13</b>	<b>12</b>	<b>12</b>	
Number of species in lakes	1	0	4	1	3	4	4	5	
Number of species in outlets	7	9	7	5	10	3	3	5	
Number of species in inlets	10	11	12	12	11	8	8	3	
Number of species in inlets and outlets	12	15	16	13	15	10	9	7	

can be observed very rarely. At the places of mass aggregations, the larvae were heavily infected with microsporidia, with the infection incidence reaching up to 40–75% (in 1982–1992, WEISER & GELBIČ, pers. comm.), while infected specimens from inlets exhibited the infection incidence very low. Larvae of *S. argyreatum* collected in Rachelsee, Čertovo, Laka, Plešné, and Prášilské lakes, as well as larvae of *S. ornatum* from Rachelsee, Kleiner Arbersee, Černé, and Laka lakes did not show any signs of infection by microsporidia in 2010 (no visible pansporoblasts in the gut; GELBIČ, pers. comm.). This low infection rate indeed may indicate a certain improvement of population fitness owing to improving environment.

The only three representatives of mosquitoes (family Culicidae, all 43 species within the Czech Republic aquatic) probably do not represent species diversity of the family within the studied lakes. Larvae of the only representative of the genus *Ochlerotatus* (subfamily Culicinae) have been collected in Laka Lake (besides its inlet and the inlet of Grosser Arbersee). Larvae of at least two species of the genus *Anopheles* (subfamily Anophelinae) were collected in inlet area of Grosser Arbersee and Kleiner Arbersee. They occurred very rarely in the inlets, perhaps incidentally, but hundreds of larvae inhabited mainly various kinds of pools near the lake shore, sometimes very small or evidently temporary. They were collected only in spring. The second second generation was not detected. There is hardly any doubt that mosquitoes of at least several species occur near all other lakes too, as documented by numerous attacks by female imagines during collecting macroinvertebrates. Their “absence” is apparently due to insufficient investigation of respective habitats.

The family Dixidae (all 10 species aquatic) is represented by two genera within the Bohemian Forest lakes. Of these, larvae of *Dixella amphibia* have been found in Plešné Lake in several specimens only. The occurrence of larvae of *Dixella* in the lakes is scarce; the species is distributed here probably owing to its rather wide ecological range (known from dystrophic and eutrophic waters; HÅLAND 2009). Larvae of the genus *Dixa* are typical inhabitants of running waters and their occurrence in Rachelsee in 2003 (JEZBEROVÁ, unpubl.) seems to be rather incidental. Recently, larvae live neither in the inlets or outlet of this lake (Table 17).

The family Ceratopogonidae (within the Czech Republic, 100 of 189 species aquatic) occurs in both the lakes and inlets/outlets across the Czech as well as German lakes (cf. Table 17). The only representative determined into the generic level, *Atrichopogon* (subfamily Forcipomyiinae) occurred solely in inlets (SENOO 2009). Number of species of the Ceratopogonidae living in the studied lakes seems to be most biased by underestimation of all remaining dipteran families due to imperfect determination. More species (e.g., of the genera *Bezzia* or *Stillobezzia* of the subfamily Ceratopogoninae) have recently been found in Alpine lakes (cf. BOGGERO & LENCIONI 2006, FÜREDER et al. 2006).

Of the family Chaoboridae (all 6 species aquatic), the only species, *Chaoborus obscuripes* (found in Laka Lake) has been determined at the species level, although at least one more species was most probably present in the lakes. The Chaoboridae represent the only dipteran families living solely in lakes, not found in inlets/outlets at all. However, its representatives were not found in Rachelsee, Prášilské, and Plešné lakes (cf. Table 17). In Laka Lake, larvae were most abundant and inhabited places of littoral densely covered with submerged vegetation, but they were rare or absent at plant-free parts of the littoral or places sparsely overgrown with vegetation. The larvae are semiplanktonic and show diurnal activity; they are hidden during daylight and active in the water column during night (BORKENT 1981). In fishless lakes in general, phantom midges as top invertebrate predators may control zooplankton size and structure (cf. RIESSEN & YOUNG 2005); however, this is not the case of most of the lakes (except for Laka Lake) in this study.

The family Blephariceridae (all 6 species aquatic) was represented by a single species, *Liponeura* sp. This finding seems to be rather incidental since larvae are specialised to live at places in streamline exposed to strong current. Several larvae were collected in outlets of Laka and Prášilské lakes only. Similarly, the only representative (*Psychoda* cf. *phalaenoides*) of the family Psychodidae (within the Czech Republic, 120 of 131 species aquatic) was found in Laka Lake outlet. Contrary to the Blephariceridae, larvae of some genera can inhabit standing waters, too. SVOBODOVÁ (2010) collected larvae of the same species and larvae of the genus *Berdeniella* sp. (subfamily Psychodinae, tribe Pericomini) downstream in outlet of Laka Lake at the distance 1.7–2.8 km from the lake.

A single representative of predominantly terrestrial family Cecidomyiidae (within the Czech Republic, only a single of 504 species aquatic, cf. ROZKOŠNÝ & VAŇHARA 2004) has been found possibly incidentally in the outlet of Laka Lake. The only known aquatic representative of the family is *Dicerura iridis* (Kaltenbach, 1874) and the material should be re-examined from this point of view.

Of the orthorhaphous families, the Empididae (within the Czech Republic, 50 of 267 species aquatic) are restricted mostly to inlets, outlets are inhabited less frequently. Although we often observed numerous swarming or foraging behaviour patterns of imagines of Empididae above open water in nearly all the lakes, their littoral is apparently not inhabited by larvae. Larvae are rather semiaquatic, but they can reach considerable densities among other “other Diptera” in inlets. Three genera have been found, *Clinocera*, *Wiedemannia*, and *Chelicerica* (Table 17).

A single finding of larva of *Rhagio* sp. (family Rhagionidae; within the Czech Republic, 2 of 24 species aquatic) in the inlet of Prášilské Lake (SENOO 2009) seems to be quite incidental or, in fact, representing some rather terrestrial species. Larvae of this genus are considered terrestrial and the family is sometimes not considered aquatic at all (cf. BULÁNKOVÁ 2003b). The only “true” aquatic genus within this family is *Chrysopilus* with two species within the Czech Republic (cf. ROZKOŠNÝ 1980, ROZKOŠNÝ & VAŇHARA 2004). There are no data on their distribution in the Bohemian Forest.

A single specimen (fully developed larva) of *Ibisia marginata* (Athericidae, all 3 species aquatic) was collected in outlet of Rachelsee (Table 17). This finding should be considered incidental, larvae of this species usually live at lower altitudes being relatively abundant there. A well-known, vulnerable species of this family, *Atherix ibis* (Fabricius, 1798) with a remarkable crowding specialisation in its reproductive biology (cf. TUŠA 1993, 1994, KUBÍK & SPITZER 2005) has not yet been found in the lake outlets. However, imagines were observed at the bridge across the Uhlava River near its confluence with the Černý Potok stream (outlet of Černé Lake) in 1995 (REISCHIG, pers. comm.) and their presence in some lake outlets seems to be likely.

The family Tabanidae (within the Czech Republic, 40 of 54 species aquatic) is represented by at least 3 species in the Bohemian Forest lakes, *Hybomitra* sp., *Tabanus* sp., and *Haematopota* cf. *pluvialis* (Table 17). A fourth species, a single female of the genus *Chrysops* (subfamily Chrysopsinae) was observed in imaginal stage attacking collectors on the shore of Kleiner Arbersee. Horseflies were restricted to the German lakes, mostly Grosser and Kleiner Arbersee, larvae have never been found in inlets/outlets. Besides relatively lower altitude, we can suppose that their occurrence might be dependent on very suitable substrate. Larvae of Tabanidae prefer soft, muddy places overgrown with mosses that are usual in these two German lakes. Elsewhere, such habitats are sufficiently developed only in Laka Lake.

The family Syrphidae (within the Czech Republic, 50 of 378 species aquatic) seems to exhibit an incidental occurrence as well. Aquatic Syrphidae are generally very rare in the

Bohemian Forest, especially at higher altitude. Moreover, larvae of numerous species require rather eutrophied habitats or habitats poor in dissolved oxygen. The only larva found in the outlet of Rachelsee at a distance of about 100 m from its beginning represents a quite exceptional finding. The outlet is probably slightly eutrophic due to touristic activities on the lake shore; stony bottom is rich overgrown by brown algae.

Of the pupiparous Diptera, only the family Muscidae (within the Czech Republic, 48 of 289 species aquatic) has been detected in the Bohemian Forest lakes. All findings (outlet of Čertovo Lake, inlets of Laka Lake, here presented as *Limnophora* sp.) probably belong to *L. riparia* known from other localities in the Bohemian Forest.

### Impact of acidification

Contrary to some Chironomidae, acid-tolerance or resistance is poorly known in other Diptera families. Literature data are very scarce and these groups are largely omitted in respective lists (e.g., RADDUM 1980, RADDUM et al. 1988, ØKLAND & ØKLAND 1986, BRAUKMANN 2001). The majority of taxa enumerated in these lists were considered acid-tolerant or even indifferent. However, Diptera were rarely evaluated at the species level, so that detailed information on acidotolerance of aquatic Diptera is in fact unknown. For instance, the representatives of the family Simuliidae are considered acid-tolerant (GUÉROLD et al. 1993, 1995, HORECKÝ et al. 2002, HORECKÝ 2003), *Wiedemannia* spp. (Empididae) and *Dicranota* spp. (Pediciidae) can even survive pH of 3.9–4.4 (HORECKÝ et al. 2002, 2006). *Pedicia* spp. of the family Pediciidae also are considered acid-tolerant (GUÉROLD et al. 1993, BULÁNKOVÁ & ZAFŮVIČOVÁ 2006), as well as some representatives of the family Ceratopogonidae (cf. also SVOBODOVÁ 2010). On the other hand, some species of *Tipula* (Tipulidae) and *Ibisia marginata* (Athericidae) can be considered acid-sensitive (cf. HORECKÝ et al. 2002).

Unfortunately, we have no more data either on a survival of atmospheric acidification by dipteran taxa other than Chironomidae, or their quantitative changes or recovery, since most data on their occurrence has been acquired during the past decade. We can only suppose that the Simuliidae (at least *Simulium argyreatum* in outlet of Prášilské Lake) survived the period of heavy acidification, because mass occurrences of blackfly larvae were observed in 1976, 1982, 1994, 1999, 2002, and 2009–2010 (SOLDÁN, unpubl.).

## Biogeographic composition of aquatic insect fauna

### Species distribution and chorology

The geographical area sizes of individual species vary considerably in extent. The factors underlying this variation remain poorly understood, and could include a number of ecological and evolutionary processes. The factors that determine an area size are usually linked to specific traits of organisms that also determine abundance (GASTON 1997, 1998), e.g., those permitting wider resource use, escape from predation, or higher competitive ability. Some authors suggested a key role of physiology in determining area size (CALOSI et al. 2010).

The fauna of the Bohemian Forest lakes is dominated by widely distributed species, those Holarctic and Palaearctic prevail (altogether 170 species, 66%; Fig. 14, Table 18). The smallest areas are exhibited by West Palaearctic species, which include about a third of the lakes' inhabitants (altogether 97 species, 34%; Fig. 14, Table 18). Most species (105 species, 41%; Fig. 14, Table 18) belong to those of the Palaearctic distribution. Naturally, there are several distribution patterns of the Palaearctic species. A considerable number of species exhibits a Transpalaearctic distribution from England and Iberian Peninsula to the Russian Far East or even Japan; other species are distributed mostly eastward to central Siberia.

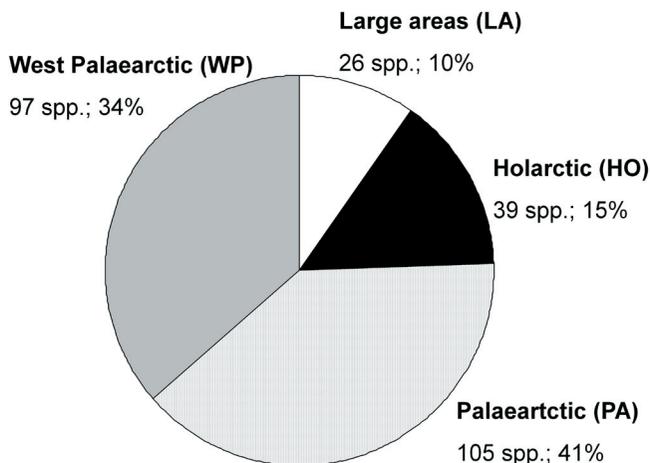
Four taxa, namely Chironomidae, Odonata, Heteroptera, and Coleoptera, include species with the largest areas, i.e. large area (LA), Holarctic (HO), and Palaearctic (PA) distribution.

**Table 18.** Numbers of species of individual groups recorded in the Bohemian Forest lakes (incl. inlets and outlets) distributed in main biogeographic regions (after DE LATTIN 1957, 1967). Abbreviations of distributional types: LA – Large area, HO – Holarctic, PA – Palaearctic, WP – Westpalaearctic.

Groups	No. of species	LA	HO	PA	WP
Ephemeroptera	19	1	2	7	9
Odonata	20	0	6	12	2
Plecoptera	32	0	1	4	27
Heteroptera	34	4	1	22	7
Megaloptera	2	0	0	0	2
Trichoptera	44	0	2	13	29
Coleoptera	57	8	6	29	14
Chironomidae	59	13	21	18	7

The family Chironomidae and the order Odonata exhibit the highest number of such species, 88 and 90%, respectively (Table 18). Other taxa (Plecoptera, Megaloptera, and Trichoptera) belong to a group with prevailing West Palaearctic distribution (84, 100, and 66%, respectively; Table 18). The order Ephemeroptera forms a transitory group exhibiting approximately a half of species with the West Palaearctic distribution (47%) and a half of species with large areas (53%; Table 18).

The cosmopolitan diptera family Chironomidae occurs in all biogeographic regions of the world, including Antarctica. They have been subject to generally accepted studies in vicariance biogeography. The best evidence is well understood austral vicariant patterns shown by the chironomids of the southern continents (see SÆTHER & EKREM 2003, KROSCHEK et al. 2011 and references herein). Such a high proportion of species with large areas is undoubtedly connected with high dispersal abilities of the group. Active individual flight appears limited to less than 10 km (McLACHLAN 1986, McLACHLAN & NEEMS 1996) and is in any case restricted by the short duration of the adult life stage (generally only a few days, OLIVER 1971). However, passive long-distance transport on wind current enables colonising new habitats rapidly (OLIVER 1971), although this manner is not directed at suitable habitats and relies on wind currents. An interesting alternative dispersal mechanism comes from evidence for survival and viability of chironomid larvae in the gut passage of migratory birds (GREEN & SANCHEZ 2006).



**Fig. 14.** Biogeographic composition of insect fauna of the Bohemian Forest lakes.

In the studied lakes, five types of distributional patterns of the Chironomidae could principally be distinguished (Table 19): (i) Species with large area (13 species) distributed besides of the Palaearctic and Holarctic region also in the Oriental region (e.g., *Limnophyes gurgicola*, *Brillia bifida*). *Eukiefferiella claripennis* and *Corynoneura scutellata* occur also in the Australian region, the latter species have been recorded even from the Neotropical region. These species are either widespread in Europe (e.g., *Procladius choreus*, *Macropelopia nebulosa*, *Ablabesmyia monilis*, *Brillia bifida*), or they are currently reported from a small number of European countries (*Procladius sagittalis*, *Conchapelopia melanops*, *Limnophyes gurgicola*). (ii) Holarctic species (21 species) either common in most of Europe (e.g., *Paratrichocladius rufiventris*, *Psectrocladius sordidellus*) or restricted to western, northern and central Europe (e.g., *Cricotopus pulchripes*, *Eukiefferiella devonica*, *Parakiefferiella bathophila*, *Paratrichocladius skirwithensis*, *Pagastiella orophila*, *Tanytarsus signatus*). (iii) Transpalaearctic species distributed throughout the whole region, extending to Far East (e.g., *Ablabesmyia phatta*, *Rheocricotopus fuscipes*). (iv) Palaearctic species (25 species), reliable distribution data of which cover western, northern and partially central Europe, seemingly uncommon in south Europe and absent in east Europe (e.g., *Heterotrissocladius grimshawi*, *Chaetocladius dissipatus*, *Psectrocladius oligosetus*, *Chironomus pseudothummi*, *Micropsectra roseiventris*, *Tanytarsus buchonius*); some of them also occur in north Africa (e.g., *Cardiocladius capucinus*, *Psectrocladius barbatipes*, *Stempellinella brevis*). (v) West Palaearctic species restricted to south-western and west-central part of Europe (*Eukiefferiella pseudomontana*, *Psectrocladius barbatipes*, *P. oligosetus*, *Pseudorthocladius filiformis*).

In contrast to Chironomidae with predominantly passive dispersal, representatives of the Odonata are distributed in large areas, partly owing to active flight ability. They can disperse by flight at the distance of tens to thousands of kilometres and/or 20° or more of latitude (TAYLOR & TAYLOR 1977, GIBO 1981, TAYLOR 1986, CORBET 1999). However, they can disperse passively, as well, using, e.g., convergent winds, thermals, or cold-air currents. Vagility of many species is extremely wide being supported also by some features of their biology. These are particularly: wide ecological range and a tendency to colonise extreme habitats in larvae, feeding and foraging habits, invasive behaviour, and tendency to territoriality and mass migrations.

In the Bohemian Forest lakes, four types of distributional patterns of Odonata could be principally distinguished (Table 19): (i) Holarctic species (6 species); most of them are circum-boreal (*Enallagma cyathigerum*, *Aeshna subarctica*, *Sympetrum danae*) and boreo-alpine (*Aeshna caerulea*). (ii) Species of the Transpalaearctic distribution (5 species), such as *Ischnura elegans*, *Lestes sponsa*, and *Cordulia aenea*. (iii) Palaearctic species (7 species), such as Ponto-Mediterranean *Ischnura pumilio* and *Pyrrhosoma nymphula*, or boreo-montane *Coenagrion hastulatum*. (iv) Only two species are of the West Palaearctic distribution (*Somatochlora metallica* and *Aeshna cyanea*).

Further two aquatic insect groups living in the Bohemian Forest lakes, namely Heteroptera (Nepomorpha and Gerromorpha) and Coleoptera (Table 19) apparently exhibit some common features as to their distribution and dispersal. They account for a great share of widely distributed species (Holarctic and Palaearctic: 79 and 75% of species, respectively). Both groups are characterised, by a relatively high vagility connected with an active and rapid flight at a distance of at least several kilometres (PAJUNEN & JANSSON 1969, SCHNEIDER 1986, BILTON 1994, LUNDKVIST et al. 2002). Most representatives are eurytopic lentic species, which are not apparently specialised on a particular habitat type. In less permanent lentic habitats, these species require a greater mobility, which indirectly results in a larger size range compared to lotic species (e.g., RIBERA & VOGLER 2000). Besides the eurytopy, these

species are abundant and/or have high area occupancy. Migration is also substantially supported by pterygopolymorphy in Heteroptera, Gerromorpha, e.g., alternation of brachypterous (apterous) and alate morphs (ANDERSEN 2000). Similarly, aquatic beetles show variation in flight muscle development, from absent to fully developed (JACKSON 1973). Among West-Palaeartic species with smaller areas, many recorded taxa are flightless or scarcely flying, which can be connected with their preference of stable habitats of running waters and springs (e.g., *Deronectes platynotus*, *Hydroporus ferrugineus*, *Elmis rioloides*; cf. WAGNER & LIEBHERR 1992, KEHL & DETTNER 2007). Moreover, the occurrence of flightless forms can be positively correlated with colder environments (JACKSON 1973).

In the Bohemian Forest lakes, eight types of distributional patterns of Coleoptera and Heteroptera could be distinguished (Table 19): (i) Species with large area (9 species of Coleoptera and 4 species of Heteroptera) distributed besides of the Palaeartic and Holarctic region also in the Oriental region (e.g., *Noterus clavicornis*, *Agabus bipustulatus*, *Corixa punctata*, *Notonecta viridis*, *Sigara lateralis*, *Aquarius paludum*). (ii) Holarctic species (6 species of Coleoptera (e.g., *Hydroporus obscurus*, *Hydrobius fuscipes*), only *Limnoporus rufoscutellatus* of Heteroptera). Some Coleoptera are absent or only restricted in occurrence in southern Europe (e.g., *Hydroporus tristis*). (iii) Palaeartic species distributed throughout the whole Europe (16 species of Coleoptera and 15 species of Heteroptera). They comprised mostly eurytopic species, which are common in most of suitable wetland habitats in Europe (e.g., *Gyrinus substriatus*, *Hydroporus palustris*, *Dytiscus marginalis*, *Anacaena lutescens* of Coleoptera, and *Hesperocorixa sahlbergi*, *S. fossarum*, *Notonecta glauca*, *Microvelia reticulata*, *Gerris lacustris* of Heteroptera). (iv) Palaeartic species distributed in western, northern and central Europe which are absent or with only very restricted occurrence in southern Europe (13 species of Coleoptera, e.g., *Hydroporus erythrocephalus*, *Agabus sturmi*, *Rhantus exsoletus*, *Enochrus affinis*, and 7 species of Heteroptera, e.g., *Cymatia bondorffii*, *Glaenocoris propinqua*, *Notonecta lutea*). (v) West Palaeartic species distributed throughout entire Europe (*Graptodytes pictus*, *Berosus signaticollis*, and *Corixa dentipes*, *Sigara nigrolineata*, *Plea minutissima*). (vi) West Palaeartic species distributed in western, northern and central Europe, which are absent or with only very restricted occurrence in southern and/or eastern Europe (7 species of Coleoptera, e.g., *Nebrioporus assimilis*, *Agabus melanarius*, *Anacaena globulus*, *Helophorus flavipes*, and *Notonecta maculata*, *Velia caprai*, *Gerris gibbifer*). (vii) West Palaeartic species distributed in western and central Europe, which are absent in northern Europe and generally also in eastern Europe (*Hydroporus ferrugineus*, *Elmis rioloides*, *Limnius perrisi* and *Micronecta scholtzi*). (viii) West Palaeartic species with restricted distribution in Europe, including central Europe (*Deronectes platynotus*, *Ilybius crassus*).

Representatives of the order Ephemeroptera of the Bohemian Forest lakes represents a transitory group, because of equal number of species distributed in large areas and in West Palaeartic. Generally, mayflies possess a very low vagility and, consequently, a large number of species exhibits small, restricted or even endemic areas (cf. HAYBACH 1998, BARBER-JAMES et al. 2008, BAUERNFEIND & SOLDÁN 2012). Extremely short life-span does not enable an active flight over long distances or to break dispersal barriers. It is also connected with relatively high speciation rate. Moreover, most species are restricted to running waters only and habitat-specialised with narrow ecological range. In fact, the studied lakes represent disturbed habitats, where mostly not specialised species are able to survive. These species are often simultaneously widely distributed. The ubiquitous *Cloeon dipterum* is the only species occupying a large area, distributed in the transitory Palaeartic-Oriental area (in India and China). *Siphonurus alternatus* and *Ephemerella mucronata* are the only Holarctic species (Table 19). The former is circum-boreal with a boreo-montane distribution in Euro-

**Table 19.** Distribution of species recorded in the Bohemian Forest lakes (incl. inlets and outlets) in main biogeographic regions (after DE LATIN 1957, 1967) (squares) and in Europe or the Westpalaearctic subregion (circles). Full and empty symbols indicate the distribution of a species in the whole region/area (global) and only in a part or a margin of the region/area, respectively; its distribution based on incomplete information is marked by a question mark. Abbreviations of distributional types: LA – Large area, HO – Holarctic, PA – Palaearctic, WE – Westpalaearctic, WP – Palaeartic, NC – North-Central European, CE – Central European/submediterranean, EE – East European (for more details, see Faunistics and biogeography in Material and methods).

Order / Species	General distribution			Distribution within Europe (WP)					Note	Distribution in the ecoregions <sup>1)</sup>
	LA	HO	PA	WP	WE	SC	NC	CE		
<b>Ephemeroptera</b>										
<i>Ameletus inopinatus</i>		□	■			○	●	○	○	Mongolian FE <sup>2)</sup> , orcotundral
<i>Siphonurus aestivalis</i>			■		●	●	●	●	●	Mongolian (?) FE, Siberian (?) FE
<i>Siphonurus lacustris</i>			■		●	●	●	●	●	Siberian FE, tundra type
<i>Siphonurus alternatus</i>		■			●	●	●	○	○	Siberian FE, boreal type
<i>Cloeon dipterum</i>					●	●	●	●	●	Polycentric species (in Europe)
<i>Baetis alpinus</i>				■	●	●	●	●	●	Holoalpine FE
<i>Baetis vernus</i>			■		●	●	●	●	●	Siberian (?) FE, polycentric (in Europe)
<i>Batis muticus</i>				■	●	●	●	●	●	Central Asian, polycentric (in Europe)
<i>Baetis rhodani</i>			□	■	●	●	●	●	●	Polycentric species
<i>Ecdyonurus austriacus</i>				■		○	●	●	○	Alpine (?) FE
<i>Ecdyonurus silvaegabretae</i>				■			●	●	●	CE endemite (?)
<i>Rhithrogena tridina</i>				■	○	●	○	○	○	Alpine FE, expansive type
<i>Rhithrogena loyolae</i>				■	○	●	○	○	○	Alpine(?), Carpathian (?) FE
<i>Leptophlebia marginata</i>			■		●	●	●	●	●	Ural FE
<i>Leptophlebia vespertina</i>			■			○	●	●	●	Ural FE
<i>Habroleptoides confusa</i>				■	●	●	●	●	●	Holomediterranean FE, expansive type
<i>Habrophlebia lauta</i>				■	●	●	●	●	●	Pontokaspian FE, expansive type
<i>Ephemerella ignita</i>			■		●	●	●	●	●	Polycentric species
<i>Ephemerella mucronata</i>			■		○	●	●	●	●	Tundra FE (circumboreal, circumtundra)
<b>Odonata</b>										
<i>Coenagrion hastulatum</i>			■		○	●	●	●	●	Boreo-montane, in Pyrennes and England
<i>Coenagrion puella</i>			■		●	●	●	●	●	Ponto-mediterranean
<i>Enallagma cyathigerum</i>			■		●	●	●	●	●	Circumboreal
<i>Ischnura elegans elegans</i>			■		○	●	●	●	●	Transpalaearctic, Ponto-mediterranean

Table 19. Continued

Order / Species	General distribution							Distribution within Europe (WP)							Note	Distribution in the ecoregions <sup>5)</sup>
	LA	HO	PA	WP	WE	SC	NC	CE	EE	EE	EE	EE	EE			
<i>Ischnura pumilio</i>			■		●	●		●	●	●				Ponto-mediterranean	1-14,16-18,X,Y	
<i>Pyrhosoma nymphula nymphula</i>			■		●	●		●	●	●				Ponto-mediterranean	1-18,22-24,X	
<i>Lestes sponsa</i>			■		●	●		●	●	●				Transpalaeartic	1-18,20,22-24,X,Y	
<i>Aeshna cyanea</i>		■		■	●	●	●	●	●	●				Boreo-alpine; glacial relict east to the Ural Mts.	3,4,8,9,11,14,18,20-23	
<i>Aeshna grandis</i>		■		■	●	●	●	●	●	●				east to the Ural Mts.	1-5,8-16,18, 20,22-25,X,Y	
<i>Aeshna juncea</i>		■		■	●	●	●	●	●	●				east to the Ural Mts.	2,4,5,7-18,20-23	
<i>Aeshna subarctica</i>		■		■	●	●	●	●	●	●				Circumboreal	1,2,4,5,8-11,14-18,20-23	
<i>Aeshna viridis</i>		■		■	●	●	●	●	●	●				Circumboreal	4,8-10,14-16,20-23	
<i>Cordulia aenea</i>		■		■	●	●	●	●	●	●				Transpalaeartic	9-11,14,23	
<i>Somatochlora metallica metallica</i>			■	■	●	●	●	●	●	●				Transpalaeartic	2,4,7-18,20,22-23,25,Y	
<i>Leucorhina dubia</i>			■	■	●	●	●	●	●	●				east to the Volga basin	4,5,7-16,18,20-25	
<i>Libellula quadrimaculata</i>		■		■	●	●	●	●	●	●				Transpalaeartic	2,4,8-10,14-16,18,20-25	
<i>Orthetrum cancellatum</i>			■	■	●	●	●	●	●	●				Siberian (?) FE east to Mongolia, Holomediterranean FE	1-18,23-25,Y	
<i>Sympetrum danae</i>		■		■	●	●	●	●	●	●				Circumboreal	1-18,20,25,X,Y	
<i>Sympetrum sanguineum</i>		■		■	●	●	●	●	●	●				Circumboreal east to western Siberia	2-4,7-18, 1-18,20-25,X,Y	
<b>Plecoptera</b>																
<i>Diura bicaudata</i>		■		■	●	●	●	●	●	●						4,8-10,17,18,20-23
<i>Chloroperla tripunctata</i>				■	●	●	●	●	●	●						1-10,17,18
<i>Siphonoperla torrentium</i>				■	●	●	●	●	●	●						1-5,7-10,13,14,16-18
<i>Brachyptera seicornis</i>				■	●	●	●	●	●	●						1,2,4-11
<i>Amphinemura standfussi</i>				■	●	●	●	●	●	●						2,4,5,7-11,13-16,18,20-23,25,Y
<i>Amphinemura sulcicollis</i>				■	●	●	●	●	●	●						1-6,8-11,13-18,20-23
<i>Nemoura avicularis</i>				■	●	●	●	●	●	●						2,4,5,8-10,13-16,18,20-23
<i>Nemoura cambrica</i>				■	●	●	●	●	●	●						1-18,20-25,Y
<i>Nemoura cinerea</i>				■	●	●	●	●	●	●						1,2,5,7-10,14,17,18
<i>Nemoura marginata</i>				■	●	●	●	●	●	●						3-10
<i>Nemurella pictetii</i>				■	●	●	●	●	●	●						1,2,4-11,13-18,20-23,25
<i>Protonemura auberti</i>				■	●	●	●	●	●	●						4-10
<i>Protonemura lateralis</i>				■	●	●	●	●	●	●						4,8
<i>Protonemura hrabei</i>				■	●	●	●	●	●	●						3-7,9,10,14
<i>Protonemura intricata</i>				■	●	●	●	●	●	●						1-11,13-16,21,23
<i>Protonemura meyeri</i>				■	●	●	●	●	●	●						1-11,13-18,20-23
<i>Protonemura montana</i>				■	●	●	●	●	●	●						2,4-10,18

Table 19. Continued

Order / Species	General distribution				Distribution within Europe (WP)						Note	Distribution in the ecoregions <sup>e)</sup>
	LA	HO	PA	WP	WE	SC	NC	CE	EE			
<i>Capnia vidua</i>				■	●	●	●	●	●	●	also Island and Novaya Zemlya	2–10,18–21
<i>Leuctra alpina</i>				■	○			●			Alpine species	3,4,8–10
<i>Leuctra aurita</i>				■	○			●				1,2,4,8–10
<i>Leuctra autumnalis</i>				■	○			●	○			4,8–10
<i>Leuctra braueri</i>				■	○			●	○			4,5,8–10
<i>Leuctra dalmani</i>				■	●			●			Balkans	4–10
<i>Leuctra digitata</i>			■	■	●	●	●	●	●		Transpalaeartic	1–18,20–25
<i>Leuctra fusca</i>				■				●				10
<i>Leuctra hippopus</i>				■	●	●	●	●	●		Near East	1–11,13–18,20–25,Y
<i>Leuctra inermis</i>				■	●	●	●	●	○			1–11,13,14,17,18
<i>Leuctra nigra</i>				■	○	●	●	●	○		missing in Iberian Peninsula	3–11,13–15,17,18,20–23
<i>Leuctra pseudocingulata</i>				■				●				4,8–10
<i>Leuctra pseudosignifera</i>				■	●			●	○			4–10
<i>Leuctra rauscheri</i>				■	●	●	●	●	○			2–4,6,8–10
<b>Heteroptera</b>												
<i>Nepa cinerea</i>			■		●	●	●	●	●		Transpalaeartic	
<i>Cymatia bomsdorffii</i>			■		●	●	●	●	●		Transpalaeartic	
<i>Glaenocoris propinqua</i>			■		○	●	●	●	●		boreo-montane, transpalaeartic	
<i>Callicoris praeusta praeusta</i>			■		●	●	●	●	●		Transpalaeartic	
<i>Corixa dentipes</i>					○	●	●	●	●		missing in the Iberian Peninsula	
<i>Corixa punctata</i>	■				●	●	●	●	○		Oriental region, East Palaeartic	
<i>Hesperocoris sahlbergi</i>			■		●	●	●	●	●		Transpalaeartic	
<i>Paracoris concinna concinna</i>			■		●	●	●	●	●		Transpalaeartic	
<i>Sigara nigrolineata</i>				■	●	●	●	●	●			
<i>Sigara limitata limitata</i>			■		●	●	●	●	●			
<i>Sigara semistriata</i>			■		●	●	●	●	●			
<i>Sigara distincta</i>			■		●	●	●	●	●			
<i>Sigara falleni</i>			■		●	●	●	●	●		missing in the Iberian Peninsula	
<i>Sigara fossarum</i>			■		●	●	●	●	●		missing in the Iberian Peninsula and Balkans	
<i>Sigara lateralis</i>	■				●	●	●	●	●		Transpalaeartic	
<i>Micronecta scholtzi</i>				■	●	●	●	●	○?		Distribution in Ukraine?	
<i>Ilyocoris cimicoides cimicoides</i>				■	●	●	●	●	●		Transpalaeartic	
<i>Notonecta glauca glauca</i>			■		●	●	●	●	●		Transpalaeartic	
<i>Notonecta lutea</i>			■		●	●	●	●	●			

Table 19. Continued

Order / Species	General distribution						Distribution within Europe (WP)						Note	Distribution in the ecoregions <sup>5)</sup>	
	LA	HO	PA	WP	WE	SC	NC	CE	EE						
<i>Notonecta maculata</i>				■	●	●	○	●							
<i>Notonecta reuteri reuteri</i>			■		●	●	●	●	●	●					boreo-montane
<i>Notonecta viridis</i>	■				●	●	●	●	●	●					Oriental region
<i>Plea minutissima minutissima</i>				■	●	●	●	●	●	●					
<i>Hebrus ruficeps</i>			■		●	●	●	●	●	●					missing in the Iberian Peninsula
<i>Hydrometra gracilenta</i>			■		●	●	●	●	●	●					missing in the Iberian Peninsula
<i>Microvelia reticulata</i>			■		●	●	●	●	●	●					
<i>Velia caprai caprai</i>				■	●	●	●	●	●	●					Oriental region
<i>Aquarius paludum paludum</i>	■				●	●	●	●	●	●					
<i>Gerris argentatus</i>			■		●	●	●	●	●	●					
<i>Gerris gibbifer</i>				■	●	●	●	●	●	●					missing in Balkans
<i>Gerris lacustris</i>			■		●	●	●	●	●	●					Transpalaeartic
<i>Gerris lateralis</i>			■		●	●	●	●	●	●					boreo-montane
<i>Gerris odontogaster</i>			■		●	●	●	●	●	●					missing in the Iberian Peninsula and Balkans
<i>Limnoporus rufoscutellatus</i>			■		●	●	●	●	●	●					missing in the Iberian Peninsula
<b>Megaloptera</b>															
<i>Stalis fuliginosa</i>				■	●	●	●	●	●	●					
<i>Stalis lularia</i>				■	●	●	●	●	●	●					
<b>Trichoptera</b>															
<i>Rhyacophila dorsalis persimilis</i>				■		○		○							3-5,9,11
<i>Rhyacophila glareosa</i>				■		○		○							4,9,10
<i>Rhyacophila obliterata</i>			■		●	●	●	●	○						Western Siberia, Altay
<i>Rhyacophila praemorsa</i>				■	○	○	○	○							2-4,8,9
<i>Philocolopis granulatus</i>			■		○	○	○	○	●						2-4,8-10,13-16
<i>Philopotamus montanus</i>			■		○	○	○	○	●						1-11,13-15,17,18,20-23
<i>Philopotamus ludificatus</i>			■		○	○	○	○	●						3,4,8-10,14,16
<i>Wormaldia occipitalis</i>				■	●	●	●	●	●	●					1-10,13-15,17,18
<i>Cynus flavidus</i>				■	○	○	○	○	●	●					4,8-18,20-23
<i>Cynus trimaculatus</i>			■		●	●	●	●	●	●					Siberia
<i>Holocentropus dibius</i>			■		●	●	●	●	●	●					1-18,20-24,Y
<i>Plectrocnemia conspersa</i>			■		○	○	○	○	●	●					2-4,8-18,20-23
<i>Plectrocnemia geniculata</i>			■		●	●	●	●	●	●					1-18,20-23
<i>Polycentropus flavomaculatus</i>			■		●	●	●	●	●	○					1-4,6,8-10,12,13,17,18
<i>Lype phaeopa</i>				■	●	●	●	●	●	●					1-5,7-11,13-18,20-23
<i>Agrypnia varia</i>			■		●	●	●	●	●	●					1,2,4-18,20-23
				■	●	●	●	●	●	●					1,3-18,20-25,Y

Table 19. Continued

Order / Species	General distribution						Distribution within Europe (WP)						Note	Distribution in the ecoregions <sup>e)</sup>
	LA	HO	PA	WP	WE	SC	NC	CE	EE	EE				
<i>Oligotricha sriata</i>				■	●	○	●	●	●	●				4-11,13-18,20-23
<i>Phryganea bipunctata</i>			■		●	○	●	●	●	●			Transpalearctic	3-5,8-18,20-23
<i>Apatania fimbriata</i>				■	○	○								4,8-11,13
<i>Drusus annulatus</i>				■	●	○								4,8-11,13,17,18
<i>Drusus chrysolus</i>				■	○	○								4,8,9,11
<i>Drusus discolor</i>				■	○	○								1-10,14,16
<i>Limnephilus centralis</i>				■	●	●	●	●	○	○				1,2,4-11,13-15,17,18,20-23
<i>Limnephilus coenosus</i>			■		●	○	●	●	●	●			Siberia (Sayany Mts.), Far East (Primorye)	2,4,7-10,13-18,20-23
<i>Limnephilus decipiens</i>			■		●	●	●	●	●	●			Turkey, Siberia	4-20,22-25
<i>Limnephilus lunatus</i>				■	●	●	●	●	●	●			Iran	1-18,20-25,X,Y
<i>Limnephilus nigriceps</i>			■		●	○	●	●	●	●				4,8-18,20-23,25
<i>Limnephilus rhombicus</i>		■			●	○	●	●	●	●				1-18,20-25,Y
<i>Rhadicoleptus alpestris alpestris</i>			■		●	○	●	●	○	○			Siberia (Sayany Mts.)	4,8,9,11,13-18,20-23
<i>Chaetopterygopsis maclachlani</i>			■		○	○	○	○	○	○			Siberia (Pribaikalie)	2,4,5,7-10,23
<i>Chaetopteryx villosa</i>				■	●	○	●	●	●	●				2,4,8-10,13-18,20-23
<i>Pseudopsilopteryx zimmeri</i>				■	○	○								4,9,10
<i>Psilopteryx psorosa bohemosaxonica</i>				■		○							Bohemian Forest, Krušné hory Mts./Erzgebirge	9
<i>Acrophylax zerberus</i>				■	○	○								2-4,9,10
<i>Allogamus uncatus</i>				■		○								3-10
<i>Halesus rubricollis</i>				■		○								4,9,10
<i>Hydatophylax infumatus</i>				■	●	○	●	●	○	○				3-5,8-10,13-18,20-23
<i>Melampophylax nepos nepos</i>				■		○								9,10
<i>Micropterna nycteroibia</i>			■		●	○	○	○	○	○			east to Central Asia	1-15,24,25
<i>Parachiona picicornis</i>				■	○	○	●	●	●	●				4,8-10,13-16,20,22,23
<i>Odontocerum albicorne</i>				■	●	●	●	●	○	○				1-5,8-11,13-18,23
<i>Molanna nigra</i>			■				●	○	○	○			boreo - montane, Siberia (Pribaikalie)	9,14-16,20,22,23
<i>Molannodes tinctus</i>			■		○	○	●	●	●	●			Transpalearctic	8-11,13-16,20-23,25
<i>Mystacides azurea</i>			■		○	○	●	●	●	●			Transpalearctic	1-18,20-25,Y
<b>Coleoptera</b>														
<i>Gyrinus marinus</i>			■		●	○	●	●	●	●			Transpalearctic	
<i>Gyrinus sibiricus</i>			■		●	○	●	●	●	●				
<i>Haliphus heydeni</i>			■		●	○	●	●	●	●				
<i>Haliphus sibiricus</i>			■		●	○	●	●	●	●				

Table 19. Continued

Order / Species	General distribution				Distribution within Europe (WP)							Note	Distribution in the ecoregions <sup>4)</sup>
	LA	HO	PA	WP	WE	SC	NC	CE	EE				
<i>Halipilus flavicollis</i>			■		●	●	○	●	●	●		missing in the Iberian Peninsula	
<i>Noterus clavicornis</i>	■				●	●	●	●	●	●		India, China	
<i>Noterus crassicornis</i>			■		●	●	●	●	●	○		missing in the Iberian Peninsula	
<i>Deronectes latus</i>				■	●	●	●	●	●	○		missing in the Iberian and Apennine Peninsulas	
<i>Deronectes platynotus platynotus</i>				■	○	○		●					
<i>Graptodytes pictus</i>				■	●	●	●	●	●	●		China	
<i>Hydroglyphus geminus</i>	■				●	●	●	●	●	●			
<i>Hydrogorus erythrocephalus</i>			■		○	○		●					
<i>Hydrogorus ferrugineus</i>				■	●	●		●					
<i>Hydrogorus incognitus</i>				■	●	●		●		○			
<i>Hydrogorus memnonius</i>				■	●	●		●		●		east to Central Asia	
<i>Hydrogorus nigrita</i>			■		●	●		●		●			
<i>Hydrogorus obscurus</i>		■			●	●		●		●			
<i>Hydrogorus palustris</i>			■		●	●		●		●			
<i>Hydrogorus planus</i>			■		●	●		●		●			
<i>Hydrogorus tristis</i>		■			●	○		●		●			
<i>Hydrogorus umbrosus</i>			■		●	●		●		●		Transpalaeartic	
<i>Hygroetus impressopunctatus</i>		■			●	●		●		●			
<i>Hygroetus versicolor</i>			■		●	○		●		●			
<i>Hyphydrus ovatus</i>			■		●	●		●		●			
<i>Nebrioporus assimilis</i>				■	●	●		●		●			
<i>Oreodytes sammar-kii sammarkii</i>			■		●	●		●		●			
<i>Agabus sturmi</i>			■		●	●		●		●			
<i>Agabus affinis</i>			■		●	●		●		●			
<i>Agabus biguttatus</i>	■				●	●		●		●		India	
<i>Agabus bipustulatus</i>	■				●	●		●		●		China	
<i>Agabus guttatus guttatus</i>			■		●	●		●		●			
<i>Agabus melanarius</i>				■	●	○		●		●			
<i>Ilybius crassus</i>				■	●	●		●		●			
<i>Rhantus exoletus</i>			■		●	●		●		●		Transpalaeartic	
<i>Rhantus frontalis</i>			■		●	●		●		●			
<i>Rhantus suturalis</i>	■				●	●		●		●		China, Australia, New Caledonia	
<i>Laccophilus minutus</i>	■				●	●		●		●		Oriental region	
<i>Dytiscus marginalis marginalis</i>			■		●	●		●		●			
<i>Helophorus flavipes</i>				■	●	○		●		●			

Table 19. Continued

Order / Species	General distribution			Distribution within Europe (WP)						Note	Distribution in the ecoregions <sup>1)</sup>	
	LA	HO	PA	WP	WE	SC	NC	CE	EE			
<i>Helophorus granularis</i>			■		●	●	●	●	●	●		
<i>Ceryon quisquilius</i>	■				●	●	●	●	●	●		Nearctic, Neotropic, Australian, and Hawaii
<i>Coelostoma orbiculare</i>			■		●	●	●	●	●	●		China
<i>Anacaena globulus</i>				■	●	○	●	●	●	○		
<i>Anacaena lutescens</i>		■			●	●	●	●	●	●		in Nearctic introduced
<i>Berosus signaticollis</i>				■	●	●	●	●	●	●		
<i>Enochrus ochropterus</i>			■		●	●	●	●	●	●		
<i>Enochrus affinis</i>			■		●	○	●	●	●	●		Transpalaeartic
<i>Hydrobius fuscipes</i>			■		●	●	●	●	●	●		
<i>Laccobius minutus</i>				■	●	○	●	●	●	●		
<i>Hydraena brittini</i>				■	●	●	●	●	●	●		
<i>Cyphon punctipennis</i>			■		●	●	●	●	●	●		Transpalaeartic
<i>Cyphon variabilis</i>	■		■		○	●	●	●	●	●		Transpalaeartic
<i>Elmis rioloides</i>				■	○	●	●	●	●	●		Neotropic, Nearctic
<i>Limnius perrisi perrisi</i>				■	●	●	●	●	●	●		
<i>Donacia obscura</i>			■		●	●	●	●	●	●		
<i>Platunmaris sericea</i>			■		●	●	●	●	●	●		
<b>Chironomidae</b>												
<i>Procladius choreus</i>	■				●	●	●	●	●	●		Far East, Oriental region, Nearctic (doubtful)
<i>Procladius sagittalis</i>	■				●	○	○	●	●	●		Oriental region
<i>Apsectrotanytus trifasciipennis</i>				■	●	○	●	●	●	○		
<i>Macropelopia adaucta</i>				■	●	○	●	○	○	○		
<i>Macropelopia nebulosa</i>	■				●	○	●	○	○	○		Oriental region
<i>Macropelopia notata</i>			■		●	○	○	○	○	○		
<i>Ablabesmyia monilis</i>	■				●	●	●	●	●	●		Far East, Nearctic, Oriental region, Neotropic (doubtful)
<i>Ablabesmyia phatta</i>				■	●	○	●	●	●	○		Far East (transpalaeartic)
<i>Conchapelopia melanops</i>	■				●	○	●	●	●	○		Oriental region
<i>Nilotanytus dubius</i>				■	●	○	●	●	○	○		Oriental region (doubtful)
<i>Nataria punctata</i>				■	○	○	○	○	○	○		Far East (transpalaeartic)
<i>Thienamimyia carnea</i>				■	●	○	○	○	○	○		
<i>Pothisia longimanus</i>	■				●	○	●	●	●	●		Far East (transpalaeartic), Nearctic, Oriental region

Table 19. Continued

Order / Species	General distribution						Distribution within Europe (WP)						Note	Distribution in the ecoregions <sup>5)</sup>
	LA	HO	PA	WP	WE	SC	NC	CE	EE					
<i>Pseudodiamesa branickii</i>	■				●	○	○	●					Far East (transpalearctic), Nearctic, Oriental region	
<i>Prodiamesa olivacea</i>		■			●	●	●	●	○				Far East (transpalearctic) Oriental region	
<i>Brillia bifida</i>	■				●	●	●	●						
<i>Cardiocladius capucinus</i>			■		●	○	○	○						
<i>Chaetocladius dissipatus</i>			■		○	○	○	○						
<i>Corynoneura lobata</i>	■				●	○	●	●	○				Nearctic, Oriental region	
<i>Corynoneura scutellata</i>	■				●	○	●	●	○				Nearctic, Australian, Neotropical, Oriental region	
<i>Cricotopus pulchripes</i>		■			●	○	●	○						
<i>Eukiefferella breviculcar</i>			■		●	○	●	●					Nearctic, Australian, Oriental region	
<i>Eukiefferella claripennis</i>	■				●	○	●	●						
<i>Eukiefferella devonica</i>		■			●	○	○	●						
<i>Eukiefferella pseudomontana</i>				■	○	○	○	○						
<i>Heterorissocladus grimshawi</i>				■	○	○	○	○						
<i>Heterorissocladus marcidus</i>	■				○	○	○	○					Nearctic, Oriental region	
<i>Krenosmittia boreoalpina</i>				■	○	○	○	○					Nearctic (doubtful)	
<i>Limnophyes gurgicola</i>	■				○	○	○	○	○				Oriental region	
<i>Orthocladus lignicola</i>			■		●	○	○	●						
<i>Parakiefferella bathophila</i>		■			●	○	●	●						
<i>Paraphaenocladus pseudirritus</i>		■			●	○	○	○						
<i>Paratrichocladus rufiventris</i>		■			●	●	○	○	○					
<i>Paratrichocladus skirwithensis</i>		■			○	○	○	○						
<i>Psectrocladius barbatipes</i>				■	○	○	○	○						
<i>Psectrocladius bisetus</i>			■		○	○	○	○						
<i>Psectrocladius oligosetus</i>			■		○	○	○	○						
<i>Psectrocladius psilopterus</i>		■			○	○	○	○						●
<i>Psectrocladius sordidellus</i>		■			○	○	○	○						
<i>Pseudorthocladus filiformis</i>				■	○	○	○	○						
<i>Rheocricotopus effusus</i>		■			○	○	○	○						
<i>Rheocricotopus fuscipes</i>		■			○	○	○	○					Far East (transpalearctic)	
<i>Ivetenia calvescens</i>			■		○	○	○	○						
<i>Chironomus pseudothummi</i>			■		○	○	○	○						
<i>Endochironomus albipennis</i>			■		○	○	○	○						●
<i>Glyptotendipes parvipes</i>		■			○	○	○	○						○

Table 19. Continued

Order / Species	General distribution				Distribution within Europe (WP)				Note	Distribution in the ecoregions <sup>*)</sup>
	LA	HO	PA	WP	WE	SC	NC	CE		
<i>Kiefferiulus tendipediformis</i>			■		●	○	○	●		
<i>Pogastrella orophila</i>		■			●	○	●	●		
<i>Phaenopsectra flavipes</i>		■			●	○	○	○	○	
<i>Polypedilum albicorne</i>		■			●	○	○	●		
<i>Polypedilum laetum</i>		■			●	○	○	○		
<i>Micropsectra atrafasciata</i>			■		●	○	○	●		
<i>Micropsectra fusca</i>				■	●	○	○	○		
<i>Paratanytarsus penicillatus</i>		■			○	○	○	○		
<i>Stempellinella brevis</i>				■	●	○	○	●		
<i>Tanytarsus buchoniis</i>				■	●	○	○	○		
<i>Tanytarsus curticornis</i>		■			●	○	○	○		
<i>Tanytarsus signatus</i>		■			●	○	○	○		
<i>Tanytarsus pallidicornis</i>		■			●	○	○	○		

<sup>\*)</sup> Bioregions according to ILLIES (1978): 1 – Iberian Peninsula including the Balearic Islands and Macaronesia; 2 – Pyrenees; 3 – Apennine Peninsula including Corsica, Sardinia, Sicily and Malta; 4 – Alps; 5 – Western Balkans (Dinarian); 6 – Western Balkans (Hellenic, Aegean); 7 – Eastern Balkans (Pontic); 8 – Western highlands; 9 – Central highlands (Hercynian); 10 – Carpathians; 11 – Pannonian; 12 – Pontic; 13 – Western lowlands; 14 – Central lowlands; 15 – Baltics; 16 – Eastern lowlands; 17 – Ireland (Ireland and Northern Ireland); 18 – England, Wales and Scotland, including the Orkney, Shetlands and Færøerne Islands; 19 – Iceland; 20 – Boreal Highlands; 21 – Tundra; 22 – Northern Sweden; 23 – Taiga (Karelian); 24 – Caucasus; 25 – Caspian Lowlands; X – North African Palaearctic region (Maghreb); Y – Asia Minor including Cyprus.

<sup>\*\*)</sup> FE – faunistic element.

pe. Seven species are Palaearctic (e.g., *Siphonurus lacustris*, *Baetis vernus*, *Leptophlebia marginata*), or even Transpalaearctic (*Ameletus inopinatus*, *Leptophlebia vespertina*, *Ephemera ignita*). *A. inopinatus* is boreo-alpine in Europe. Nine species are West Palaearctic. There are widely distributed and abundant species (e.g., *Baetis rhodani*, *Habroleptoides confusa*, *Habrophlebia lauta*) and species with restricted area (e.g., *Rhithrogena* spp.). Two species, *Ecdyonurus silvaegabretae* and *E. austriacus*, are probably endemic in central Europe.

The last group of studied taxa consists of the orders dominated by West Palaearctic species. These are Megaloptera (100%), Plecoptera (84% of species), and Trichoptera (66%). Except for some Trichoptera, representatives of these groups are generally bad fliers with a considerably restricted life-span. Most dispersers are concentrated within 10–20 m distance of the stream post-emergence and seldom fly more than 100 m perpendicular to the stream channel (e.g., SODE & WIBERG-LARSEN 1993, GRIFFITH et al. 1998, PETERSEN et al. 1999). Although some imagines of stoneflies can be captured over than 500 meter or even a kilometer from the stream, 90% of imagines are usually trapped within 11 m (BRIERS & GEE 2004, MACNEALE et al. 2005). Moreover, dispersal in some stoneflies is apparently restricted by brachyptery of males (e.g., *Capnia* and *Diura*). Strong fliers such as many large Limnephilidae and Hydropsychidae caddisflies were found to disperse several kilometers from their native habitats (e.g., CRICHTON & FISHER 1982, KOVATS et al. 1996) and thus are considered good dispersers (SODE & WIBERG-LARSEN 1993). Flying ability is not the only factor determining the area size of species of these groups. The majority of species with large areas belongs to habitat generalists that often have flexible life-cycles and/or occur in large quantities (GRAF et al. 2009, 2008). In contrast, species with restricted areas often include habitat specialists with fixed life cycles. Distribution of many mountain species is undoubtedly influenced by historical events, such as speciation in isolated mountain ranges or periglacial survival and dispersion from refugia.

There are no species with large areas and only three Holarctic species in the Bohemian Forest lakes (stonefly *Diura bicaudata*, and caddisflies *Limnephilus nigriceps* and *L. rhombicus*; Table 19). Altogether 13 species of caddisflies are Palaearctic (mostly Limnephilidae, Polycentropodidae and Phryganeidae: *Limnephilus coenosus*, *Polycentropus flavomaculatus*, *Phryganea bipunctata*). Four Palaearctic stoneflies simultaneously represent abundant species of a wide ecological range with really Transpalaearctic distribution (*Amphinemura standfussi*, *Nemoura cinerea*, *Nemurella pictetii*, *Leuctra fusca*). Within West Palaearctic species altogether 12 species of caddisflies and 8 species of stoneflies are distributed almost throughout the whole Europe (Table 19). Some species restricted to central Europe and close adjacent areas (8 species of caddisflies, e.g., *Rhyacophila glareosa*, *Apatania fimbriata*, *Halesus rubricollis*, *Melampophylax nepos*, and 5 species of stoneflies, e.g., *Leuctra pusilla*, *L. pseudocingulata*, *Protonemura lateralis*). Six species of stoneflies (e.g., *Leuctra alpina*, *L. aurita*), and caddisflies *Rhyacophila praemorsa* and *Drusus annulatus* are distributed predominantly in central and west Europe, and caddisfly *Allogamus uncatus* in central and southeastern Europe. Caddisfly *Wormaldia occipitalis* is distributed in the whole Europe except for its eastern parts and eight stoneflies (e.g., *Brachyptera seticornis*, *Protonemura montana*) and remaining species of caddisflies (e.g., *Plectrocnemia geniculata*) are distributed in the whole Europe except its eastern and northern parts (Table 18).

### Distributional patterns

To analyse biogeographic composition of insect fauna of the Bohemian Forest lakes, we evaluated the distribution of species within Europe separately in detail. Of the total 267 species evaluated (Table 19), we have selected 253 species with sufficient information on

**Table 20.** Numbers of species recorded in the Bohemian Forest lakes (incl. inlets and outlets) distributed in Europe or the Westpalaeartic subregion.

Distributional type	No. of species
West-Central	23
North-Central	12
East-Central	4
South-Central	8
Central	21
West-Central + North-Central	28
West-Central + South-Central	9
South-Central + East-Central	1
North-Central + East-Central	9

their areas. Of these, 138 species show almost equal distribution within the whole Europe (i.e. occur in four or five European subareas, Table 19). These species mostly belong to largely distributed (Palaeartic, Holarctic, and large area species) and rather eurytopic and abundant species able to inhabit a wide extent of aquatic habitats. The remaining 115 species have restricted areas. Species occurring only in central Europe or in closely adjacent areas show the most restricted areas (CE = 21 species, Table 20). This group consists mainly of stoneflies (e.g., *Leuctra pseudocingulata*, *L. pusilla*, *Protonemura lateralis*) and caddisflies (e.g., *Pseudopsilopteryx zimmeri*, *Halesus rubricollis*, *Allogamus uncatatus*). Some species can be even considered endemic in this area (*Ecdyonurus silvaegabretae*, *E. autriacus*, *Psilopteryx psorosa bohemosaxonica*). The share of east European species is very low (EC = 4 species, SC+EC = 1 species, Table 20). In fact, there are no species with a typical eastern European or eremial (steppe) distribution and Carpathian species do not reach Hercynian mountains. The only “eastern” species extending to the Bohemian Forest lakes are species with circum-boreal distribution pattern (NC+EC = 9 species, Table 20), such as *Aeshna subarctica*, *Enallagma cyathigerum*, and *Ephemerella mucronata*, and species with boreo-montane distribution pattern, such as *Glaenocoris propinqua*, *Molanna nigra*, *Molannodes tinctus*, and *Ilybius crassus* (NC = 12 species, Table 20). Atlantic or west European elements have a considerable influence on the composition of the Bohemian Forest lakes fauna. There are two principal components of this group of species: (i) West-Central species (WC = 23 species, Table 20). Some of them show the eastern border of their areas just in the Bohemian Forest (e.g., *Eukiefferiella pseudomontana*) or they extend eastward to Slovakia and Hungary (several chironomids, e.g., *Cardiocladius capucinus*, and a caddisfly *Drusus annulatus*). (ii) West-Central species extending to Fennoscandia (WC+NC = 28 species, Table 20; e.g., the beetle *Hydroporus incognitus*) or to Mediterranean (WC+SC = 9 species, Table 20; e.g., the stoneflies *Leuctra rauscheri*, *Chloroperla tripunctata*, the aquatic bug *Micronecta scholtzi*, and the caddisfly *Plectrocnemia geniculata*). Species with Mediterranean distribution extended to central Europe, such as the mayflies *Rhithrogena iridina* and *R. loyolaea*, and the beetle *Elmis rioloides* are relatively rare (SC = 8 species, Table 20).

Generally, the area of the Bohemian Forest including the glacial lakes represents a “crossroad”, meeting all possible European distributional types with the exception of eastern European. They are situated within the eastern border of the area of west European (Atlantic) species, within the northern border of south European (submediterranean) species and within the southern border of north European species (e.g., boreo-montane species).

The most important historical event forming the areas of recent fauna of the lakes was the last Pleistocene glaciation. Lasting for about 110 000 years including short warmer period of about 20 000 years (Riss-Würm interglacial), this glaciation (called also Würm or Wisla glaciation) terminated about 15–10 thousand years ago. The maximum southern border of

continuous glacier reached the Krkonoše (Giant) Mts. in the Sudetes and the Carpathians in the last but one, third glaciation (Riss), enabling more free area shifts thanks to more favourable climatic conditions (OHLEMÜLLER et al. 2012). The Bohemian Forest was not continuously covered with ice. There is geological evidence for 10–11 relatively small glaciers at the highest altitudes of the Bohemian Forest that had directly formed corries of the lakes closing them by face moraines with some boulders greater than 1 m<sup>3</sup>. For instance, two glaciers on Grosser Arber Mt. caused the formation of Grosser Arbersee and Kleiner Arbersee, three glaciers were formed on Rachel Mt., where only one lake (Rachelsee) has been preserved (RATHSBURG 1930, CHÁBERA 1975, VESELÝ 1994). Using the dating of the Grosser Arbersee sediments by the <sup>14</sup>C methods, the beginning of the postglacial period started up 9600–10 000 years ago (MICHLER 1984); the emergence of Plešné Lake has been dated to 14.2 thousand years ago (TÁTOŠOVÁ et al. 2006). The studied lakes and their fauna could be affected also by a large but isolated glacier in the Alps. Generally, post-glacial aquatic fauna can be characterised as “mixed” (“glaziale Mischfauna”) consisting of species withdrawing from the area with continuous glaciation (“nördliche Gletcherrandarten”) and species withdrawing to the north from isolated but progressive glacier of the Alps (“südliche Gletcherrandarten”) according to THIENEMANN (1950).

Direct consequence of glacier oscillation and withdrawal northward was the extinction of not only rests of Tertiary thermophilous fauna but also of most other elements, except for resistant eurytherm species (VIETS 1940). Only a small number of them reached southern or Mediterranean refuges due to west-east mountains range orientation. However, there is only limited information on the late- and post-glacial origin of aquatic insects. It is assumed that the main glacial refuges are primarily situated in three main European peninsulas, Iberia, Italy, and the Balkans, from which species had the potential to re-colonise Europe since the last glaciation (cf. OHLEMÜLLER et al. 2012). Climate-based analysis of glacial source locations also provides support for the existence of central-western European areas, in which temperate species could have persisted, and northern areas, in which particularly boreal species could have persisted during the last glacial maximum (OHLEMÜLLER et al. 2012). Occurrence of both temperate and boreal species north of the main mountain chains are generally considered to be spatially limited, occupying small areas of favourable microclimate and supporting relatively small populations (STEWART & LISTER 2001, RULL 2009). One of the small and patchy areas with high glacial source potential may have been located in the central European lowland northwards of the Alps (OHLEMÜLLER et al. 2012), which may serve as refuges for the Bohemian Forest fauna.

Comparing the areas of distribution of central European Trichoptera, MALICKY (1983) found that their refuges do not correspond with any known biome type (= “Biochore” according to DE LATTIN 1967), i.e. Arboreal, Oreotundral, and Eremial. Thus, the new biome type, Dinodal, outside of any refuge in central Europe has been proposed (MALICKY 1983, 2006) and recently confirmed by molecular analyses (e.g., PAULS et al. 2006, LEHRIAN et al. 2009, PREVIŠIĆ et al. 2009).

### **Species protection of aquatic insect fauna**

The Bohemian Forest glacial lakes are unique relict aquatic habitats, which are undoubtedly inhabited by specific assemblages rarely observed elsewhere in the Czech Republic. Naturally humic waters are known to host communities adapted to low pH, often with a high conservation value. Although the lakes were subjected to strong anthropogenic acidification, their fauna is worth of attention from the point of view of species protection. According to the current Red List of Invertebrates of the Czech Republic (FARKAČ et al. 2005), 30 of 302 species found in total are threatened (Table 21). However, there are several insect families

(e.g., Chironomidae) not evaluated in FARKAČ et al. (2005) due to insufficient knowledge on distribution and ecology of their species. On the contrary, the knowledge on the distribution and actual imperilment of many species has been extended since 2005. Moreover, several species were newly recorded from the Czech Republic. Therefore the protection status of selected species should be re-evaluated.

In mayflies, predominantly eurytopic species were found due to high sensitivity of the group to acidity. Only one species, *Rhithrogena loyolae*, has been classified to be vulnerable in FARKAČ et al. (2005) (Table 21). It is relatively abundant and widespread in other European areas, e.g., in the Tatra Mts., the Alps, and the Pyrenees (BAUERNFEIND & SOLDÁN 2012). In the Czech Republic, however, it is very rare (ZAHRÁDKOVÁ et al. 2009) that might be connected with acidification of Hercynian mountains. Two species were recorded in the Czech Republic after 2005, *Ecdyonurus silvaegabretae* and *Ecdyonurus* cf. *austriacus*. The former has been newly described from several localities in the Bohemian Forest (SOLDÁN & GODUNKO 2006). Although its geographic distribution is not known in detail, its present area shows some distributional restriction. The larvae are specialised to clear epirhithral stream habitats and are likely sensitive to organic pollution. These reasons classify the species as vulnerable. *Ecdyonurus* cf. *austriacus* shows similar limitations like *E. silvaegabretae*, however, species delimitation remains still not clear (SOLDÁN et al. 2008) (Table 21). Therefore, this species rather belongs to the data deficient category. *Siphonurus alternatus* represents a relict boreo-montane species, which has limited occurrence in the Czech Republic (ZAHRÁDKOVÁ et al. 2009). Czech Bohemian Forest lakes are situated on or near the southern border of its European subarea. Due to its sparse occurrence, it is suggested to be classified near threatened. Considering the Red List of mayflies of Germany (MALZACHER et al. 1998), *Ameletus inopinatus* is evaluated endangered in Germany, where it lives near its southern area border.

In Odonata there are two critically endangered species, *Aeshna caerulea* and *Ae. subarctica* (Table 21). These species have been classified critically endangered due to their restriction to several local populations in mountain areas and their high sensitivity to any anthropogenic activities (DOLNÝ et al. 2007). Two vulnerable species (*Ae. juncea* and *Leucorrhinia dubia*) and one near-threatened species (*Coenagrion hastulatum*) are especially endangered due to habitat loss and degradation of wetlands (DOLNÝ et al. 2007). The occurrence of *Ae. viridis* is not confirmed in the Czech Republic, therefore, finding of larvae in the Čertovo Lake outlet justifies its preliminary classification to the data deficient category.

With the exception of a few eurytopic species, all representatives of the order Plecoptera are highly sensitive to any changes of their habitats and all types of pollution. Thus, it is complicated to strictly define the categories of protection in individual species. The only criterion to solve this problem is evaluation of long-term changes of their distribution. Recently, we have acquired sufficient data describing major changes of taxocenoses in the past hundred years (BOJKOVÁ et al., 2012). Generally, some species do not change their distribution, though they are rare. Conversely, others originally very abundant have substantially decreased their areas, although they are still rather common in the Czech Republic. These species should be considered near-threatened. Moreover, several species included in the Red List (FARKAČ et al. 2005) require a re-classification, because they are not actually disappearing or their present distribution is suggesting that they are more frequent than supposed earlier. *Diura bicaudata* and *Siphonoperla torrentium* showed no distributional changes (BOJKOVÁ et al., 2012), while *Capnia vidua* and *Leuctra pseudosignifera* were found at numerous new localities (earlier they were probably overlooked due to their emergence in late winter or early spring). Consequently, the above mentioned species should be excluded from the Red List. *Leuctra pusilla* was included in the Red List as *Leuctra handlirschi*, which

**Table 21.** Red-list species found in the Bohemian Forest lakes (including inlets and outlets; see Table 1 for lake codes). Full circles indicate the species listed in the red-list of invertebrates of the Czech Republic by FARKAČ et al. (2005), empty circles the species not included in this list; question mark indicates disputable species or species with proposed change of the category of protection status. Occurrences of species in German lakes are in brackets because they should be evaluated according to German red-list. Abbreviations of protection status categories: RE – Regionally extinct, CR – Critically endangered, EN – Endangered, VU – Vulnerable, NT – Near threatened, DD – Data deficient.

Order / Species	Lake(s)	RE	CR	EN	VU	NT	DD
<b>Ephemeroptera</b>							
<i>Siphonurus alternatus</i>	PL, PR, LA					○	
<i>Ecdyonurus silvaegabretae</i>	LA				○		
<i>Ecdyonurus austriacus</i>	CT						○
<i>Rhithrogena loyolae</i>	LA				●		
<b>Odonata</b>							
<i>Coenagrion hastulatum</i>	PL, (GA, KA, RA)					●	
<i>Aeshna caerulea</i>	PL, PR, (RA)		●				
<i>Aeshna juncea</i>	PL, PR, LA, (GA, KA, RA)				●		
<i>Aeshna subarctica</i>	CN, PL		●				
<i>Aeshna viridis</i>	CT						○
<i>Leucorrhinia dubia</i>	CN, (KA)				●		
<b>Plecoptera</b>							
<i>Diura bicaudata</i>	CN, CT, PR, LA, (GA, KA)					●?	
<i>Siphonoperla torrentium</i>	PR, LA, (GA, KA)					●?	
<i>Chloroperla tripunctata</i>	CT				●		
<i>Amphinemura standfussi</i>	CT, PR, LA, (RA)				●		
<i>Capnia vidua</i>	CN, CT, LA, (GA, KA)			●?			
<i>Leuctra alpina</i>	PL, LA				●		
<i>Leuctra pseudosignifera</i>	CN					●?	
<i>Leuctra pusilla</i>	CN, PL, PR, LA, (GA, KA, RA)					●	○
<b>Heteroptera</b>							
<i>Cymatia bondsdorffi</i>	LA, (GA)			●			
<i>Glaenocoris propinqua</i>	all lakes			●			
<i>Corixa dentipes</i>	PL, PR, LA					●	
<i>Sigara semistriata</i>	PL, PR, LA, (GA, KA, RA)				●		
<i>Notonecta lutea</i>	LA, (GA)				●		
<i>Notonecta reuteri</i>	CN			●			
<i>Gerris lateralis</i>	PL			●			
<b>Trichoptera</b>							
<i>Plectrocnemia geniculata</i>	CN, CT, PR				●		
<i>Drusus chrysotus</i>	CN						○
<i>Acrophylax zerberus</i>	CN, LA			●			
<i>Molanna nigra</i>	CN, CT, PR, (GA)		●				
<i>Molannodes tinctus</i>	PL, LA, (KA)			●			
<b>Coleoptera</b>							
<i>Deronectes latus</i>	CN, CT, PL, PR, (KA, RA)				●		
<i>Nebiopporus assimilis</i>	PR	●	○				
<i>Ilybius crassus</i>	PR, LA, (GA, KA, RA)				●		
<i>Cyphon punctipennis</i>	PR, (RA)				●		
<i>Donacia obscura</i>	LA, (GA, KA, RA)			●			
<b>Chironomidae</b>							
<i>Heterotrissocladius grimshawi</i>	CN, CT, PL?, LA, (GA, KA, RA)			○			
<i>Psectrocladius barbatipes</i>	LA			○			
<i>Pagastiella orophila</i>	(KA)			○			

actually does not occur in the Czech Republic. The distribution of *L. pusilla* in the Czech Republic is not known in detail; therefore the species rather belongs to data deficient category (Table 21). Several other species recorded from the Bohemian Forest lakes probably could be re-classified based on the comparison of historical and present data.

Seven rare species of water bugs are included in the Red List (FARKAČ et al. 2005). Four of them are considered endangered (*Cymatia bonsdorffii*, *Glaenocorisa propinqua*, *Notonecta reuteri* and *Gerris lateralis*), two vulnerable (*Sigara semistriata* and *Notonecta lutea*), and one near threatened (*Corixa dentipes*) (Table 21). *G. propinqua* is the most remarkable water bug species of the Bohemian Forest lakes that harbour its only large population in the country. This pelagic species swims in open water zone of cold oligotrophic waters without fish (or with sparse fish occurrence, HENRIKSON & OSCARSON 1978). Such habitats are very scarce in the Czech Republic, thus, it is pleasing that this species is quite common in all the studied lakes at present. This unique case likely has been the consequence of acidification, which caused the past fish extinction in the lakes (VRBA et al. 2003a), on the one hand, and the ongoing biological recovery, which obviously provides more abundant prey for the population increase in some acidotolerant top predators (beetles and bugs, HENRIKSON & OSCARSON 1978, CARBONE et al. 1998), on the other hand. The conservation of *G. propinqua* will depend on preserving the natural state of the lakes without fish stocking in the future. Other recorded rare water bugs are confined to oligo- to dystrophic and/or peaty habitats. *Cymatia bonsdorffii*, *Notonecta reuteri*, and *N. lutea* are strictly tyrophilous in central Europe and their occurrence is known in the Bohemian Forest peat bogs; the lakes are rather marginal habitats for them. Both mentioned backswimmers prefer littoral habitats with peat mosses, while *C. bonsdorffii* requires vertical substrates for perching, usually plants but occasionally also large stones (TULLY et al. 1991, KMENT & SMÉKAL 2002). The boreo-montane species *G. lateralis* is a poor competitor, which prefers small shaded pools without other *Gerris* species. Its suitable habitats are in the vegetated littoral developed along gentle banks with small pools among macrophyte beds (VEPSÄLÄINEN 1973, KMENT & SMÉKAL 2002). Except *Glaenocorisa propinqua*, all the mentioned endangered water bug species of the studied lakes require well-preserved natural littoral with aquatic vegetation, but without inappropriate management measures in the future, such as sediment removal or water level fluctuation.

In Trichoptera, from 46 species recorded only four species are included in the Red List (FARKAČ et al. 2005) (Table 21). The boreo-montane *Molanna nigra* was classified critically endangered. It originally occurred in Grosser Arbersee, Černé, Čertovo, and Prášílské lakes, (KLAPÁLEK 1903, NOVÁK 1996) and was proved only from Prášílské Lake at the end of the last century. Recently, it was re-collected also from Čertovo Lake and Grosser Arbersee. Ongoing investigations will probably provide a better basis for classification of this species. Similarly, the endangered *Acrophylax zerberus*, known only from a few earlier records, was recently collected in several lake inlets and outlets. *Molannodes tinctus* was classified endangered due to decreased frequency in comparison with the first half of the 20<sup>th</sup> century. A vulnerable species *Plectrocnemia geniculata* is a rare species which inhabits undisturbed spring habitats. *Drusus chrysotus* is known only from a single very recent record from the Czech Republic (CHVOJKA et al. 2009). This locality probably lies on the limit of its area and the species should be treated as data deficient at present.

Five species of aquatic beetles are classified threatened: one critically endangered, one endangered, and three vulnerable (Table 21). The diving beetle *Nebrioporus assimilis* was considered regionally extinct in the Czech Republic since the only record was based on an old undated material probably from the Brdy Mts. collected before 1961 (BOUKAL et al. 2007). At present, Prášílské Lake is the only place of its recent occurrence in the Czech

Republic. Consequently, its status should be changed from regionally extinct to critically endangered (BOUKAL et al. 2012). Since the species is known from surrounding countries, its occurrence in the Czech Republic is limited mostly by the lack of suitable well-preserved habitats of oligotrophic lakes and rivers with sandy bottom. The vulnerable diving beetle *Deronectes latus*, which prefer oligotrophic smaller streams in central Europe, is distributed locally at higher altitude across the entire Czech Republic (BOUKAL et al. 2007). The remaining three threatened species, *Ilybius crassus*, *Cyphon punctipennis*, and *Donacia obscura*, are tyrphophilous and are typical inhabitants of peaty habitats with well-preserved specific vegetation beds at higher altitude. Their distribution in Europe shows a boreo-alpine pattern. In the Czech Republic, they are mainly distributed in Bohemia (BOUKAL et al. 2007). The protection of all mentioned species in the Czech Republic is possible only by strict conservation of their mostly relict habitats and preventing the changes of their water regime, habitat degradation and pollution.

The chironomid fauna of the Czech Republic is relatively poorly known in comparison with neighbouring countries, despite the long tradition of study. Chironomidae of many aquatic habitats have not been studied yet, and the current check-list does not include a number of quite common species. The insufficient data do not allow the outline of distributional patterns and/or the estimate of population sizes of individual species. Therefore, the first proposal of the chironomid classification for the Red List (Table 21) could comprise three species with relatively known ecology and distribution. *Heterotrissocladius grimshawi* is considered to be indicative for cold, well-oxygenated conditions in European lakes, but it is absent in the Carpathian lakes (TATOLE 2004, BITUŠÍK 2004). Thus its distributional limit in south-eastern Europe is most probably located in the Czech Republic. *Psectrocladius* (*Mesopsectrocladius*) *barbatipes* prefers probably cold mountain lakes; for example, it was found being one of the indicative species for subalpine lakes in the Tatra Mts. (BITUŠÍK et al. 2006). One can suppose that the Bohemian Forest lakes provide the only habitats for the both above mentioned species in the Czech Republic. *Pagastiella orophila* is generally indicative of shallow dystrophic lakes with naturally low pH. It seems that the species has been negatively affected by strong anthropogenic acidification; consequently, the recent findings in the lakes are rare.

Considering data from the neighbouring Bavaria (ORENDT & REIFF 2003), the following taxa could be included in the list as well: *Macropelopia notata*, *Chaetocladius dissipatus*, *Krenosmittia boreoalpina* and *Micropsectra fusca*, but further information on their distribution in the Czech Republic are needed.

### **Classification of the lakes based on aquatic insects**

On the basis of the cluster analysis of recent species data (altogether 196 species), the Bohemian Forest lakes were classified into four subgroups on an arbitrary chosen level of 50% of dissimilarity of assemblages. There is a group of five Czech lakes, on one the hand, and a group of three German lakes, on the other (Fig. 15). The former consists of two subgroups, the two largest lakes (Černé, Čertovo) and three remaining Czech lakes (Prášilské, Plešné, Laka). The German lakes comprise a subgroup consisting of Grosser Arbersee and Kleiner Arbersee, and Rachelsee dissimilar to all other lakes (Fig. 15). The same grouping of the lakes was obtained when the whole dataset including historical data was analysed. Separate analyses of the dataset of benthic littoral assemblages (Ephemeroptera, Odonata, Plecoptera, Trichoptera, Megaloptera, and Diptera), and the dataset of actively moving/swimming littoral assemblages (Heteroptera and Coleoptera) resulted to the same dendrogram as well (results not shown). It indicates high invariability of the grouping of lake insects, which is similar even in different ecological groups of insects.

Černé and Čertovo lakes possess virtually the same aquatic insect assemblages (Fig. 15), despite the affiliation to different river basins (the Elbe River and the Danube River, respectively). It is caused by a high similarity of their littoral zones and their proximity. The littoral of both lakes is almost without any vegetation and bottom substrate is dominated by inorganic particles (sand, gravel, and boulders) with organic debris. These lakes are deepest and about twice larger than all other lakes by area, but one-order-of-magnitude larger on the volume basis, with the longest retention times (cf. Table 1), and are thus the most oligotrophic among the lakes (Table 2). Contrary to all other lakes, their bedrock consists of pure mica-schist (Table 1). The lakes are recently inhabited by 70 species, 15 species (21%) of which were not found in other lakes. Assemblages of these lakes differ from the others by the frequent presence of lotic species in the lake littoral, which is caused by a coarse substrate identical or very similar to surrounding streams. Typical examples are *Sialis fuliginosa*, *Agabus guttatus*, and *Deronectes latus*, common in the most inlets and outlets of the lakes, and an abundant population of *Nemoura avicularis*, which is a stonefly inhabiting predominantly rhithral streams, yet occurring in oligotrophic lakes, as well. Populations of *Sialis fuliginosa* and *S. lutaria* in these lakes were the most abundant compared to other lakes.

The subgroup of the remaining Czech lakes (Prášílské, Plešné, Laka) represents the lakes of different size, depth, water volume, bedrock (granite, mica-schist, and gneiss; Table 1) and also water chemistry (Table 2). The assemblages of these lakes are yet similar to the oligotrophic Černé and Čertovo lakes. All Czech lakes share 50 species. Of these, 34 species are shared by all subgroups of lakes. Prášílské, Plešné, and Laka lakes are characterised by the littoral dominated by *Carex rostrata*, especially in Laka Lake. Yet the stony, gravel, and/or coarse-sand bottom rich in organic debris is frequent in both Plešné and Prášílské lakes. Altogether 136 species were recently found in the subgroup of Prášílské, Plešné, and Laka lakes, 49 (36%) of them exhibit a unique occurrence in this subgroup of lakes. The majority of them are common inhabitants of different types of standing waters with rich emerged vegetation (e.g., *Microvelia reticulata*, *Corixa punctata*, *Hydroporus incognitus*). Most of them are rather eurytopic. Such species (e.g., *Leptophlebia marginata*, *Nepa cinerea*, *Hydroporus planus*, *Dytiscus marginalis*, *Chaoborus obscuripes*) were found especially in Laka

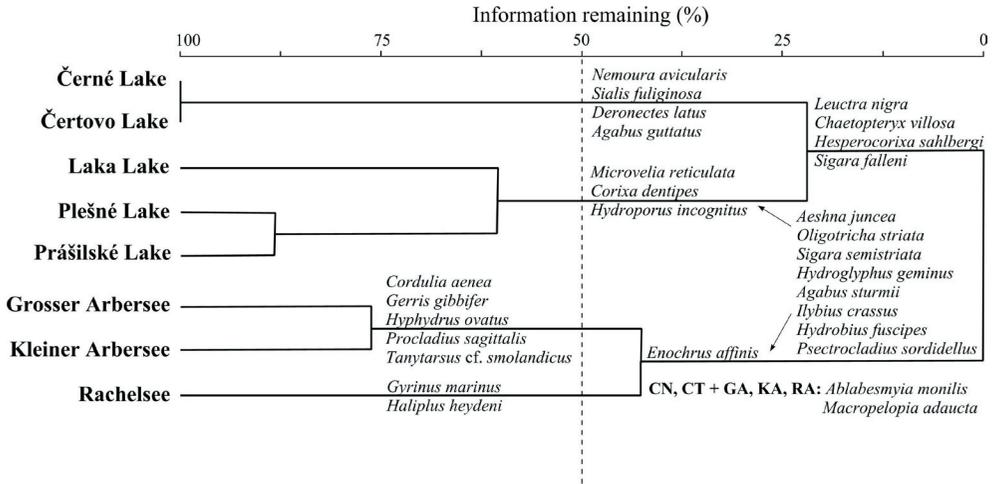


Fig. 15. Cluster analysis of the Bohemian Forest lakes based on recent presence-absence data using Ward's method and Bray-Curtis index of similarity. Dash line indicates cut level. Species unique for individual groups and pairs of groups of lakes are listed; only species present in all lakes of the group/a pair of lakes and absent in all other lakes are given.

Lake, which is the shallow and least acidified lake with highly developed littoral and emergent vegetation. Due to apparently convenient conditions and pronounced recovery from acid stress, some upstream immigrants can survive and reproduce in Laka Lake and in the upper part of its outlet, as documented by the example of Ephemeroptera. Two species (*Siphonurus aestivalis* and *Leptophlebia marginata*) commonly occurring at lower altitudes appeared in the lake during the past decade. Two rare species (*Rhithrogena loyolaea* and *Ecdyonurus silvaegabretae*) apparently have migrated upstream to the upper part of outlet recently. Further similar successful migrants are *Rh. iridina*, *Habrophlebia lauta*, and *Ephemerella mucronata* that have inhabited the Laka outlet. The second group includes all German lakes, which are very dissimilar to those Czech (Fig. 15). German lakes are characterised by similar areas, depths and water volumes, and by identical composition of the bedrock (Table 1). They differ from the Czech lakes by substantially higher amount of organic matter in the bottom substrate and waterlogged bryophytes and sedges, which are favourable for dragonfly larvae and many aquatic beetles. Therefore, the assemblages of the German lakes are characteristic of lower shares of Ephemeroptera, Plecoptera, and Heteroptera, for which the shallow littoral with deep organic sediment is not suitable, and more dragonflies and aquatic beetles than in Czech lakes (Fig. 16). Many of the 26 species (25% of all species found in German lakes) not found in Czech lakes prefer shallow, muddy, and organic or peaty substrate (e.g., *Coenagrion puella*, *Gerris gibbifer*, *Hydroporus obscurus*, *Helophorus granularis*, *Enochrus affinis*, and Tabanidae). German lakes share 70 species with the Czech lakes with sedge littoral (Plešné, Prášílské, Laka) and only 40 species (yet 34 of them are shared by all lake subgroups) with the Czech lakes with inorganic littoral (Černé, Čertovo). The former species are predominantly acid-tolerant (or tyrophilous), preferably occurring in the littoral with rich vegetation (e.g., *Aeshna juncea*, *Sigara semistriata*, *Ilybius crassus*, *Donacia obscura*).

Within the group of German lakes, Grosser Arbersee and Kleiner Arbersee have dissimilar assemblages to Rachelsee. This is probably caused by substantially lower altitude and unique character of the littoral (dominated by bryophytes) of both Grosser Arbersee and Kleiner Arbersee. Moreover, Rachelsee was strongly acidified in the past and originally rather species-poor, as was shown in crustacean species richness (VRBA et al. 2000, 2003a). This lake hosts a species-poor benthic assemblage (only 58 species/taxa found, Table 5). It consists only of acid-tolerant (or indifferent) and eurytopic species, which are not characterised by any specific characteristics.

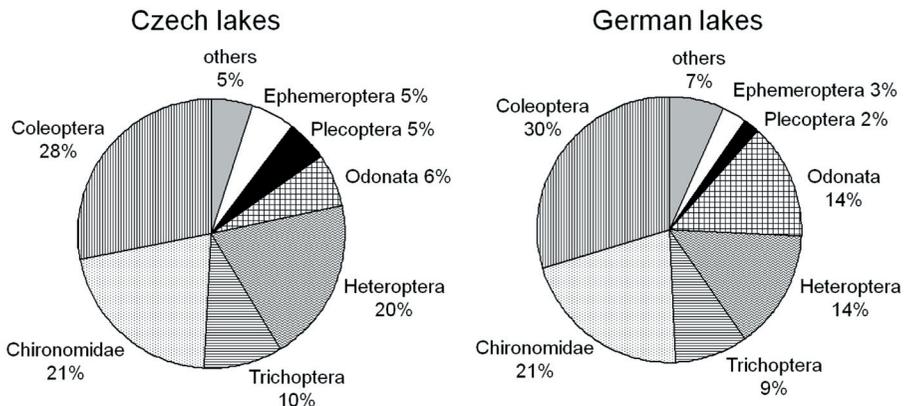


Fig. 16. Shares of aquatic insect groups in the assemblages of German and Czech lakes (only recent data were used).

The results of cluster analyses did not show a similarity of aquatic insect assemblages according to a current acidification status of lakes, demonstrating the importance of other environmental factors for aquatic insects. The chronically acidified lakes (Černé, Čertovo, Plešné, and Rachelsee) are present in all subgroups of lakes; Rachelsee is very dissimilar to all others (Fig. 15). Surprisingly, the similar, least acidified lakes (Laka, Grosser Arbersee, Kleiner Arbersee) are not grouped either. On the other hand, lake littoral characteristics are probably not the only governing factors for benthic assemblages. This is indicated by the species composition of the sedge-dominated littoral of Rachelsee, which is more similar to peat-moss-dominated Grosser Arbersee and Kleiner Arbersee than to Plešné and Prášilské lakes. Likewise, the fauna of the shallow Laka Lake is not similar to other lakes possessing large shallow littoral vegetation belts (Grosser Arbersee and Kleiner Arbersee).

Our results do not correspond with the classification of the Bohemian Forest lakes based on pupal exuviae of Chironomidae (BITUŠÍK & SVITOK 2006). The disagreement of classifications is obvious, because samples of pupal exuviae describe the chironomid assemblages of the whole lake, including sub-littoral and profundal zones, unlike benthic assemblages sampled only in the littoral zone. BITUŠÍK & SVITOK (2006) stressed the importance of geographic position (longitude or altitude) of lakes and their alkalinity for lake chironomids. However, both longitudinal and altitudinal gradients are very short in the Bohemian Forests lakes and can be the surrogates of other unmeasured factors. The longitudinal gradient is within one degree ( $13^{\circ}07'$ – $13^{\circ}52'$ ) and even less if the outlying Plešné Lake is excluded (cf. Fig. 1). The altitudinal gradient is less than 200 m. Our results suggested a prevailing influence of littoral substrate on benthic assemblages.

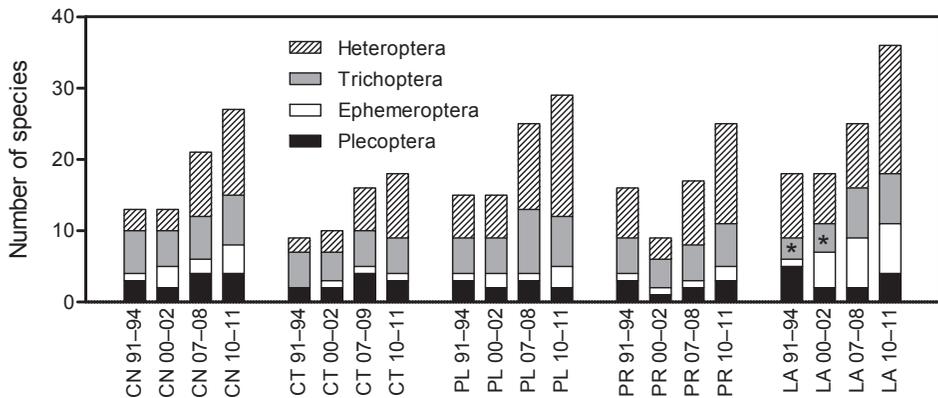
### **Tracking trends of recovery of Ephemeroptera, Plecoptera, Trichoptera, and Heteroptera in past two decades**

Reductions in the deposition of acidifying compounds across Europe (STODDARD et al. 1999, KOPÁČEK & VESELÝ 2005) led to consequent widespread chemical recovery of inland surface waters (EVANS et al. 2001). Biological recovery, however, has followed up with a time lag, taking place apparently slower than chemical recovery, and still remains less pronounced (e.g., MONTEITH et al. 2005, NEDBALOVÁ et al. 2006, ORMEROD & DURANCE 2009). Naturally, a detection of biological recovery depends on the choice of indicator and the choice of habitat (stream, pond or lake, littoral or pelagic zone). Organisms with short generation times, high dispersal abilities, and propagule banks are expected to recover relatively rapidly from stress (FINDLAY 2003). Habitats with long water retention time (lakes) are less dynamic and their biological recovery is probably more lagged than in habitats with relatively short water retention time (streams). Generally, phytoplankton and zooplankton often show early signs of recovery strongly related to increases in pH (STENDERA & JOHNSON 2008, GRAY & ARNOTT 2009 and further references herein). Data on the recovery of benthic macroinvertebrates from lakes are scarce and often equivocal (e.g., HYNYNEN & MERILÄINEN 2005, LENTO et al. 2008, STENDERA & JOHNSON 2008). In streams, there is an evidence of recovery demonstrated by re-occurrence of sensitive species (e.g., ALEWELL et al. 2001, RADDUM et al. 2001, TIPPING et al. 2002, ORMEROD & DURANCE 2009). Several factors may confound recovery of invertebrates. These are especially inadequate supply of colonists due to regionally impoverished diversity or remoteness of habitats, bottom-up processes, input of toxic metals, and episodic events resetting the system to pre-recovery levels (YAN et al. 2003). Moreover, invertebrate assemblages established during the acid phase can be resistant to change and impede re-colonisation by acid-sensitive taxa (LEDGER & HILDREW 2005).

Biological recovery can be indicated by decreased predominance of acid-tolerant taxa, re-colonisation of acid-sensitive taxa, and increased species richness and diversity (e.g.,

GRAY & ARNOTT 2009). We expected, however, that the appearance of sensitive species in the Bohemian Forest was definitely not a sufficient indicator of biotic recovery of macroinvertebrates, because the lakes were humic before anthropogenic acidification (VRBA et al. 2000). Both scarce pre-acidification pH data since the 1930s (for review, see VRBA et al. 2000) and backward pH modelling of lake water since 1850 (MAJER et al. 2003) suggested a natural acidity of some Czech lakes (e.g., Čertovo and Plešné). Therefore, the resident macroinvertebrate biota likely was influenced by naturally lower pH. This was indicated by the pre-acidification macroinvertebrate data, although they were fragmentary. The Ephemeroptera, Plecoptera, and Trichoptera (EPT) taxocenoses of the studied lakes have been continuously composed of highly-tolerant and tolerant species (classified according to SCHARTAU et al. 2008), or tolerant, resistant, and very resistant species (according BRAUKMANN & BISS 2004). In this case, indicator values of acidity developed for different European regions generally corresponded. Clear-water and humic lakes probably have different reference conditions and response to acidification (cf. SCHARTAU et al. 2008, MCFARLAND et al. 2010). However, any comparisons of reference assemblages, impacts of acidification, and the course of recovery in humic and clear-water lakes are not available. We expected that the effect of acidification was smaller in humic (i.e. naturally acid) waters, because acidification metrics based on benthic macroinvertebrates were found to be higher in humic than in clear waters at given pH (SCHARTAU et al. 2008, MOE et al. 2010). Naturally acid waters host macroinvertebrate assemblages of different composition but similar species richness (DANGLES et al. 2004). It can be connected with ameliorating effects of DOC on the toxicity of metals, such as aluminium (DRISCOLL et al. 1980), and evolved adaptation and/or exaptation of some macroinvertebrates to low pH in naturally acid waters (cf. DANGLES et al. 2004, PETRIN et al. 2007). We expected that the role of acid-sensitive species was not so crucial in the biological recovery as in clear-water lakes, because original taxocenoses were very likely composed of the species able to tolerate natural level of acidity. We have fragmentary information on pre-acidification biota (or reference conditions) of the Czech (but not German) lakes and no information on total species richness of original taxocenoses. Thus, it is hard to determine the target taxocenoses, in which successful recovery results. Our data allow us to infer indirectly the recovery processes based on comparison of species richness of different groups.

In the present study, we have selected the EPT taxa and true water bugs (Heteroptera: Nepomorpha) to demonstrate a recovery process of the Bohemian Forest lakes (Fig. 17). EPT



**Fig. 17.** Number of species of the Ephemeroptera, Plecoptera, Trichoptera, and aquatic Heteroptera found in selected (Czech) Bohemian Forest lakes in the past twenty years (periods 1994–1996, 2000–2002, 2007–2008, and 2010–2011). \* indicates insufficient sampling of the group leading to lower number of species recorded.

taxa were chosen owing to sufficient long-term data, i.e. they had been sampled during the past 20 years, yet we did not know the original composition EPT taxocenoses in detail. Moreover, rather unequal attention has been paid to the Czech compared to German lakes; the latter have been more intensely sampled only recently, i.e. within some five past years. We also added true water bugs, because they represent an insect group with quite different dispersal ability or vagility compared to EPT taxa and they have good predispositions for acidotolerance due to their hard cuticle and way of air breathing from extra body air bubble removable on water surface. The results concerning Heteroptera, however, should be evaluated with respect to different sampling frequency and methods. While samples were collected by a metal strainer in the 1990s, light traps have recently been employed. Despite using these different techniques, quite the same spectrum of species has been ascertained (PAPÁČEK et al. 2009). The only differences were in abundance of individual species.

The numbers of Plecoptera and Trichoptera species did not change in past twenty years (Fig. 17) and all the species found were present in the lakes before acidification (Tables 8, 13). Ephemeroptera showed slight increase of the number of species apparent in all lakes. *Leptophlebia vespertina* re-colonised the most acidified Čertovo Lake. Several mayflies (*Cloeon dipterum*, *Ameletus inopinatus*, *Siphonurus lacustris*, and *S. alternatus*) slightly increased the number of species in the chronically acidified Černé and Plešné lakes. The least acidified Laka Lake was most diverse and species-rich. All the above mentioned species plus *Siphonurus aestivalis*, *Baetis vernus*, and occasionally *Leptophlebia marginata* occurred there. Within the EPT taxa, mayflies are generally considered to be the most acid sensitive group. However, the acid sensitivity of mayflies as a whole used to be mostly determined on the basis of study of strongly sensitive species mainly inhabiting running waters (BRAUKMANN 2001). The above mentioned species of *Cloeon*, *Siphonurus*, and *Leptophlebia* possess a relatively wide ecological range enabling colonisation of new habitats (various standing water habitats) and also to tolerate slightly or moderately acidified habitats. Moreover, the increase in some species of mayflies can be caused also by some other effects that superimpose those of acidification (and chemical recovery). The findings of the second (late summer) generation of *Siphonurus* can indicate some changes in thermal regime of the lakes, likely influenced by a recent increase in the regional average temperature (cf. KETTLE et al. 2003).

The largest changes in species richness were found in water bugs (Fig. 17). Recent taxocenoses have a higher species richness and different composition than those inhabiting the lakes twenty years ago. The number of recorded species markedly increased in all Bohemian Forest lakes. Several species, known from a single or few lakes in the 1990s, were recently recorded from the majority or all lakes (Tables 9, 10). Eight true water bug species were recorded in the lakes before 1999 and further twelve species, i.e. nearly 52% of nepomorphan species were discovered in the lakes during last ten years. These species were found in the littoral zone of lakes and included eurytopic (or relatively eurytopic) species, such as *Sigara falleni*, *S. lateralis*, *S. striata*, and *Micronecta sholtzi*, as well as, in a lesser extent, stenotopic species (*Notonecta reuteri*). There are three groups of species as to utilising a habitat as follows: (i) They (or some of them) are really new inhabitants of the lakes and, due to their vagility and flight ability, invade new habitats offering utilizable food and suitable environment for reproduction and development. (ii) They (or rather some of them) are original inhabitants, who had so low population density ten to twenty years ago that they were not discovered by hand net collecting method. Their recent findings can reflect an increase in their population density, as well as higher probability to collect them. (iii) Some of newly found species use lakes only casually as “stepping stones” of their dispersion (e.g., a single record of *Notonecta maculata*, *N. reuteri*, and *N. viridis*). We can suppose that these changes

follow the food web changes started by recovery of plankton diversity and density (VRBA et al. 2003a, NEDBALOVÁ et al. 2006).

To conclude, a certain degree of recovery has undoubtedly been achieved in the Bohemian Forest lakes as documented by changes in some water chemistry parameters as well as an increase in species diversity (at least in Ephemeroptera and aquatic Heteroptera). However, we are not able to define the apparent progress of the recovery process and/or to predict its rate and possible termination.

Obviously, an increase in pH alone does not necessarily imply adequate water quality for macroinvertebrates. For instance, pH can increase in the acidified lakes, but it can remain below the biological threshold of many organisms (cf. FÖLSTER et al. 2007, JOHNSON et al. 2007). Besides other harmful effects, we believe that the effects of aluminium remain one of the key factors structuring recent taxocenoses of the Bohemian Forest lakes (VRBA et al. 2006). Literature data suggest that Al effects are most pronounced for, e.g., the most sensitive mayflies species (HERRMANN & ANDERSON 1986, HERRMANN 1987a); however, there are no precisely defined toxic doses for survival of macroinvertebrates (for review, see ROSSELAND et al. 1990). ROSSELAND et al. (1990) considered that fish were affected by inorganic Al concentrations  $>25 \mu\text{g.l}^{-1}$ ; an upper threshold of  $75 \mu\text{g.l}^{-1}$  was suggested as a limit for strong effects. The range of inorganic Al, i.e. the sum of ionic and particulate Al ( $\text{Al}_i + \text{Al}_p$ ) recently measured in the Bohemian Forest lakes reached  $55\text{--}383 \mu\text{g.l}^{-1}$  (Table 2). Thus, four recovering (Grosser Arbersee, Kleiner Arbersee, Laka, Prášílské) lakes showed concentrations  $>25 \mu\text{g.l}^{-1}$  and four chronically acidified (Rachelsee, Černé, Čertovo, Plešné) lakes well above  $75 \mu\text{g.l}^{-1}$ . Most of the acidic tributaries still deliver to the lakes high amounts of  $\text{Al}_p$ , which precipitates, at pH  $\sim 5$  or higher, in the littoral and/or epilimnion (VRBA et al. 2006). Such  $\text{Al}_p$  precipitates are harmful for breathing of fish (ROSSELAND et al. 1990 and references herein). In macroinvertebrates, the mechanism of effect of aluminium seems to be different. Survival of the mayfly *Leptophlebia marginata* was not affected by the different kinds of Fe-precipitations on the body and gills. Frequent moulting did not allow for an incrustation of more than 50% of the body (GERHARDT & WESTERMANN 1995). The same can be applied to aluminium as well. Moreover, it is possible that invertebrates (e.g., mayflies) are able to clean gill membranes from mucus accumulations and/or Al hydroxide precipitates (HERRMANN & ANDERSON 1986).

Beside direct toxic effects of  $\text{Al}_i$  and  $\text{Al}_p$ , the Al concentration affects other biological processes such as energy consumption in stoneflies and caddisflies (RADDUM & STEIGEN 1981), reduced  $\text{Na}^+$  haemolymph content and air-breathing in mayflies (HERRMANN 1987b) and, at least, in some water bugs as found in the water boatman *Corixa punctata* (WITTERS et al. 1984), impaired osmoregulation and ion transport (HERRMANN & ANDERSON 1986), and possibly also reproduction. The effect of aluminium on respiration rates seems to be different in the individual species used in experiments. Oxygen consumption rates were decreased in dragonflies (*Libellula julia*, *Somatochlora cingulata*), unaffected in a caddisfly (*Limnephilus* sp.), and increased in mayflies (*Heptagenia fuscogrisea*, *H. suphurea*, *Ephemera danica*; CORREA et al. 1985, 1986, HERRMANN & ANDERSON 1986, ROCKWOOD et al. 1990). Effects of metals might also cause behavioural changes. The mayfly *Leptophlebia marginata* lost its escape behaviour, when exposed to iron and lead, the effects being more pronounced at low than at circumneutral pH for both metals (GERHARDT 1994). Likewise, the detritivorous species exposed to low pH showed reduced feeding activity (JANSSENS DE BISTHOVEN & GERHARDT 2003). These results demonstrate a wide spectrum of the effects of acidity on species life-history, fitness, behaviour, and physiology, which cannot affect survival of the species directly but can have various sub-lethal consequences.

## Species (taxa) richness in the Bohemian Forest lakes in comparison with some other European lake districts

### Total species (taxa) richness

First of all, we should emphasise that the species richness of aquatic insects exhibited in the Bohemian Forest lakes seems to be high in comparison with any glacial lakes or other lake districts studied recently in Europe (Table 22). This fact concerns not only the total number of species (taxa) found, but also number of species detected within the individual groups studied (Table 23). Indeed, species richness of insects recently collected in the Bohemian Forest lakes (196 species/taxa found recently) is very high, taking into account a very small number of eight lakes only. A diversity of more than 100 insect species per area studied is rather exceptional (see Table 22). The highest species richness were found in the Alps: 112 species were reported by BOGGERO & LENCIONI (2006) in the Swiss and Italian Alps, and 114 species were collected by FÜREDER *et al.* (2006) in lakes of the Alps in Switzerland and Tyrol (both in Austria and Italy). Over one hundred taxa (106 species) were found also in lakes in Scotland by KERNAN *et al.* (2009a). The most comprehensive comparison of the diversity of benthic invertebrates in European remote lakes was published by FJELLHEIM *et al.* (2009) who reported only 110 species/taxa found in 126 lakes in the alpine zone from seven mountain lake districts throughout Europe, from central Norway through the Alps and the Carpathians to Balkans, the Retezat and Rila Mountains.

However, direct comparison of these data with the diversity found in the Bohemian Forest lakes is not possible without rarefaction analysis to compare species richness among areas with not comparable number of lakes. The number of lakes investigated was highly different, from 2 to 126 lakes, samples were taken in different seasons by different methods, and determination levels were different as well. Nevertheless, about two hundred species found in only eight lakes compared to about one hundred species found in several tens lakes (Table 22) showed remarkably different diversity of the Bohemian Forest lakes from any lake district across Europe. These differences are emphasised taking into account the share of common species, which ranges only from 10–20% (Table 22). However, this comparison is approximate again, because of very different determination levels. More than 80% of taxa of the Bohemian Forest lakes were determined to the species level, contrary to generic or even family levels used in several studies. Moreover, a great number of species known from the Bohemian Forest lakes were not collected in any of the European lakes under comparison.

The answer to the question on the causes of very high species richness of aquatic insects in the Bohemian Forest lakes is rather complex. Besides the state of knowledge of the respective lake systems, there are some objective factors like different altitude, geographic position (e.g., orography, geological and glaciation history, and the effects of climate), historical formation of fauna (e.g., effects of faunistic centres, refuges and biocentres with biocorridors, migrations and invasive behaviour), and trophic relationships (e.g., predatory pressure of fish and density of plankton). There are also factors of subjective nature like different points of view in lake/outlet/inlet definition, different sampling methods and timing and, last but not least, different data processing.

In the following six rather arbitrarily defined **items**, we attempt discussing some of these factors with regards to high species richness of the studied lakes and explain, at least partially, considerable differences in comparison to other European lake districts that single the Bohemian Forest lakes out of them:

**(i) Habitat definition and delimitation**, or habitat preferences undoubtedly play a substantial role in species richness evaluation. The crucial question is whether to include, besides the inhabitants of the littoral bottom, also those of the inlet(s) flowing through the litto-

ral and those of the water surface and open water, which occur in the lake littoral irregularly. If not, species richness would be substantially lower.

There are several groups of species, the habitat preference of which does not correspond to a typical “lake littoral benthic inhabitant”. They can be defined as follows:

(a) Temporal inhabitants (or visitors) that do not reproduce or oviposit in lake littoral habitats. This group comprise species with extremely (Odonata) or very high (Heteroptera and some Coleoptera) vagility and numerous typical lotic species (Ephemeroptera and Plecoptera), which are drifted to the lake littoral near the inlet’s mouth. They do not only persist there for a long time, but are able to finish their development and their imagines naturally migrate to oviposit to inlets again. Although these species are mostly not permanent inhabitants of the littoral zone, they undoubtedly affect the respective assemblages through, e.g., food webs and energy flow.

(b) Species tending to live in the profundal zone (i.e., below euphotic zone) of lakes (such as some Chironomidae, e.g., *Heterotrissocladius*, *Chironomus*, *Phaneopsectra* spp., *Sergentia* cf. *coracina*). The presence/absence of such species in the lake littoral mostly depends on their abundance and substrate preferences. Some species, such as *Sialis* spp., are considered typical littoral taxocene members but can be found at 7–20 m in profundal habitats (cf. DU BOIS & GEIGY 1935, BERG & PETERSEN 1956). In such cases, it is difficult to distinguish, whether a species belongs to “littoral” or “profundal” representatives, even if it lives within a transition zone.

(c) Species living on the surface of water, in fact do not enter the water column and sometimes represent semiaquatic (or semiterrestrial) forms or species preferring open water column. Semiaquatic bugs (Heteroptera, Gerromorpha) comprise species living on the free water surface often far from the lake shore (e.g., Gerridae), species preferring places near the shore and water line (e.g., Veliidae), or rather semiterrestrial species, living among emerged parts of aquatic plants (e.g., Hydrometridae). Some species even show an ability to combine water surface and diving way of life (e.g., pleustonic beetles of the family Gyrinidae).

(d) Inhabitants of open water are, e.g., an aquatic bug, *Glaenocorisa propinqua* and larvae of phantom midges (*Chaoborus* spp.). These species occur irregularly in the lake littoral in connection with their diurnal activity, thus, can be detected rather incidentally, and also their abundance detected need not reflect their actual abundance in the lake.

(e) Species that do not fit any of the above categories. Representatives of the beetle family Chrysomelidae (subfamily Donaciinae) are typical example of such aquatic insects. Their larvae live in plant tissues of submerged part of aquatic plants, imagines live on emerged parts of plants; this group is usually not considered to belong to aquatic beetles (cf. BOUKAL et al. 2007). Similarly, Diptera larvae of “piercers”, which firmly attach to plant tissues, are difficult to detect as well.

To conclude, we believe that “true lake littoral” assemblages (or communities) can hardly be defined and species richness cannot be detected if some of the above groups of species were omitted in the evaluation. The habitat preferences of most species (as well as their way of life) are overlapping and although some species live temporarily in the lake littoral zone, they represent an overall part of the whole ecosystem. As soon as any group of species is neglected, resulting diversity will inevitably decrease.

**(ii) Geographic attributes of lake districts.** There is a significant level of variation in species composition of lake communities accounted for the geographical component, which is not shared by the environmental variables. This may be a biogeographic signal or some local key signals (JOHNSON & GOEDKOOP 2000, KERNAN et al. 2009c). Regional differences

**Table 22.** Seven selected lake districts investigated throughout Europe in 1991–2011, individual lake numbers of respective species (taxa) diversity in comparison with littoral species (taxa) diversity of eight Bohemian Forest Lakes.

Reference	Investigated region (its elevation if stated)	Number of habitats	Total taxa	Common taxa	Most frequent taxa	Species richness of insect orders / notes
HEINO (2008)	Oulankajoki River basin (N-E Finland) (lowland altitudes)	48 lakes	40	25 (12%)	<i>Ephemera</i> , <i>Caenis</i> , <i>Cloeon</i> , <i>Leptophlebia</i> , <i>Somatochlora</i> , <i>Mystacides</i> , <i>Psectrocladius</i> , <i>Dicrotendipes</i> , <i>Cladotanytarsus</i> , <i>Procladius</i> , <i>Clintanypus</i> , <i>Culicoides</i> , <i>Chrysops</i>	Taxa listed only at the generic level.
BRODERSEN et al. (1998)	Danish lakes (lowland altitudes)	39 lakes (stony littoral only)	76	27 (13%)	<i>Tinodes waeneri</i> , <i>Cricotopus</i> , <i>Dicrotendipes</i> , <i>Oulimnius</i> , <i>Ceratopogonidae</i> , <i>Glyptotendipes</i> , <i>Microtendipes</i> , <i>Caenis horaria</i> , <i>C. luctuosa</i> , <i>Athripsodes cinereus</i> , <i>Cladotanytarsus</i> , <i>Cyrmus flavidus</i>	Diptera (32 taxa), Trichoptera (24), Ephemeroptera (6), Coleoptera (6), Odonata (2), Plecoptera (2), Heteroptera (2), Megaloptera (1), Neuroptera (1)
KERNAN et al. (2009)	Scotland Lake District (Scotland, UK) (518–956 m a.s.l.)	30 lochs	106	39 (19%)	<i>Polycentropus flavomaculatus</i> , <i>Ameletus inopinatus</i> , <i>Heterotanytarsus apicalis</i> , <i>Procladius</i> , <i>Capnia atra</i>	Diptera (66), Trichoptera (18), Ephemeroptera (8), Plecoptera (11), Megaloptera (1), Coleoptera (1), Heteroptera (1)
KOWNACKI et al. (2000)	Tatra Mts. (Poland) (1657–1784 m a.s.l.)	4 lakes	40	16 (8%)	<i>Microspectra radialis</i> , <i>Heterotrissocladius marcidus</i> , <i>Zavrelimyia</i> , <i>Cricotopus</i> gr. <i>fiscus</i> , <i>Macropelopia</i> , <i>Corynoneura</i>	Diptera (24), Coleoptera (9), Plecoptera (5), Trichoptera (2)
KRNO (1991)	Tatra Mts. (Slovakia) (1311–2157 m a.s.l.)	51 lakes	66	29 (15%)	<i>Ameletus inopinatus</i> , <i>Capnia vidua</i> , <i>Nemurella pictetii</i> , <i>Apatania fimbriata</i> , <i>Acrophylax</i> , <i>Drusus trifidus</i> , <i>Agabus bipustulatus</i>	Ephemeroptera (6), Odonata (4), Plecoptera (9), Trichoptera (26), Diptera (2), Coleoptera (16), Heteroptera (2), Megaloptera (1) Chironomidae not included.
KRNO (2006); KRNO et al. (2006)	High Tatra Mts. (Poland, Slovakia) (1579–2157 m a.s.l.)	45 lakes	79	33 (17%)	<i>Heterotrissocladius marcidus</i> , <i>Corynoneura</i> , <i>Microspectra</i> , <i>Capnia vidua</i> , <i>Nemurella pictetii</i> , <i>Ameletus inopinatus</i> , <i>Allogamus</i> , <i>Agabus bipustulatus</i> , <i>Apatania fimbriata</i>	Ephemeroptera (2), Plecoptera (9), Trichoptera (11), Diptera (43), Coleoptera (12), Heteroptera (1), Megaloptera (1)
ČIAMPOROVÁ- ZATŮVICOVÁ et al. (2010), ČIAMPOROVÁ- ZATŮVICOVÁ (2011)	High Tatra Mts. (Slovakia) (1677–2157 m a.s.l.)	4 lakes	81	12 (6%)	<i>Capnia vidua</i> , <i>Nemurella pictetii</i> , <i>Nemoura cinerea</i> , <i>Baetis alpinus</i> , <i>Acrophylax zerbensis</i> /sowai, <i>Hydroperus mannonius</i> , <i>Pseudodiamesa branickii</i> , <i>Prodiamesa olivacea</i> , <i>Heterotrissocladius marcidus</i>	Diptera (44), Plecoptera (14), Trichoptera (12), Coleoptera (5), Ephemeroptera (5), Megaloptera (1)
MARCHETTO et al. (2009)	Alps (Italy, Austria, and Switzerland) (1592–2796 m a.s.l.)	72 lakes	74	10 (5%)	<i>Microspectra radialis</i> , <i>Tanytarsus</i> cf. <i>tugens</i> , and <i>Zavrelimyia</i> sp.	Considered only taxa accounting more than 3% in any sample and more than 1% in at least 3 samples. Only Chironomidae treated in detail.

Table 22. Continued

Reference	Investigated region (its elevation if stated)	Number of habitats	Total taxa	Common taxa	Most frequent taxa	Species richness of insect orders / notes
FÜREDER et al. (2006)	Alps (Italy, Switzerland, and Austria) (1840–2796 m a.s.l.)	55 lakes	114	35 (17%)	<i>Corynoneura arctica</i> , <i>Paratanytarsus austriacus</i> , <i>Zavrelimyia</i> , <i>Cricotopus</i> , <i>Paratanytarsus</i> , <i>Prodiamesa olivacea</i> , Hydroptorinae	Ephemeroptera (2), Plecoptera (6), Odonata (2), Heteroptera (2), Coleoptera (11), Trichoptera (19), Diptera (74)
BOGGERO & LENCIONI (2006)	Rhaetian Alps, Pennine- Lepontine Alps (Switzerland, Italy) (1909–2571 m a.s.l.)	21 lakes	112	36 (17%)	Chironomidae dominating in all types of habitats; littoral: chironomidae 30.3– 96.6%, Trichoptera 0.6–82.7%, Plecoptera 0.0–42.4%	Ephemeroptera (2), Plecoptera (5), Odonata (2), Heteroptera (1), Coleoptera (11), Trichoptera (10), Diptera (81)
OERTLI et al. (2008)	Cirque of Macum, Swiss National Park (Switzerland) (2480–2714 m a.s.l.)	25 ponds	47	19 (9%)	<i>Agabus bipustulatus</i> , <i>Hydroporus foveolatus</i> , <i>Helophorus</i> , <i>Acrophylax zerberus</i> , <i>Limnephilus coenosus</i> , Tipulidae, <i>Bryophlaenocladus</i> , <i>Heterotrissocladus marcidus</i> , <i>Limnophyes</i> , <i>Pseudodiamesa nivosa</i> , <i>Zavrelimyia</i> cf. <i>melanura</i>	Diptera (34), Coleoptera (8), Trichoptera (3), Plecoptera (1), Heteroptera (1)
DE MENDOSA & CATALAN (2010)	Pyrenees (France, Spain) (five altitudinal categories: <1900 m, 1900–2200 m, 2200–2500, 2500–2800, >2800 m a.s.l.)	82 lakes	85	34 (16%)	Tanypodinae, Tanytarsini, Orthocladinae, Chironomini, <i>Statis</i> , Polycentropodidae, Dytiscidae	Determined at family or genus level: Odonata (2), Ephemeroptera (4), Plecoptera (7), Coleoptera (8), other Diptera (8), Trichoptera (10), Chironomidae (45)
FJELLHEIM et al. (2009)	Seven “Lake Districts”: Central Norway (CN), Italian Alps (IA), Julian Alps, Slovenia (JS), Polish Tatras (PT), Slovakian Tatras (ST), Retezat Mts., Romania (RR), Rila Mts., Bulgaria (RB) (from 728 m a.s.l. in CN to 2,535 m a.s.l. in RB)	126 lakes: CN: 24 IA: 45 JS: 14 PT: 23 ST: 16 RR: 21 RB: 29	110 45 30 23 16 21 29 18	20 (10%) 10 (5%) 14 (7%) 11 (5%) 10 (5%) 4 (2%) 6 (3%)	<i>Allogamus</i> sp., <i>Zavrelimyia</i> , <i>Heterotrissocladus marcidus</i> , <i>Microspectra</i> , <i>Macropelopia</i>	Diptera (81), Trichoptera (14), Plecoptera (7), Ephemeroptera (3), Coleoptera (3), Megaloptera (1), Heteroptera (1)
<b>Present study</b>	Bohemian Forest lakes (935–1087 m a.s.l.)	8 lakes	196	–	Altogether 215 species/taxa found in 1848–2011; 196 species out of them found in 2003–2011.	Diptera (136), Coleoptera (68), Trichoptera (49), Plecoptera (37), Heteroptera (35), Odonata (22), Ephemeroptera (20), Megaloptera (2), Neuroptera (1)

may be due to inherent variations in the nature of mountain catchments across Europe. Naturally, the location of lake systems (e.g., altitude, latitude, longitude, and distance to the sea) and characteristics of catchments (e.g., bedrock and catchment land-use) determine the nature of lake habitats and, consequently, the biota. In addition, general geographic and hydrologic characteristics, like maximum altitude and altitudinal range of the lake district, lake areas and volumes, whether are part of a chain or headwater lakes, and the lake system orientation, can influence the similarity of biota between individual lake districts. However, there is a significant level of collinearity among various explanatory variables (habitat, catchment, and geographical characteristics), so that it may not be clear whether predictors reflect ecological processes or the role of a surrogate variable (cf. KERNAN et al. 2009c).

The lake biota studied (planktonic crustaceans, rotifers, littoral invertebrates, and subfossil chironomids, diatoms or cladocerans) differed in three distinct limno-regions above a timberline: nordic (Scotland and Norway), sub-arctic (northern Finland), and alpine (the Pyrenees, the Alps, the Carpathians, and the Rila Mts.). Lake littoral invertebrates differed between Scotland, central Norway and northern Finland, and central and southern Europe, whereas the lakes of the Tatra Mts. were distinct from other central European lakes (KERNAN et al. 2009c). In our opinion, the Bohemian Forest lakes cannot be ranked to any of the above limno-regions, not only due to their lower altitude. Littoral invertebrates of our lakes have been very dissimilar to any limno-region and, simultaneously, similar in the same (but very low) degree to any limno-region (Table 22). The Bohemian Forest lakes are remote, single headwater bodies in rather separated, forested catchments. They are characterized by low altitudinal range, relatively long distance to the sea, variable catchment geology, and low number of lakes (Table 1). The geographic attributes themselves do not separate the Bohemian Forest from other lake districts but contribute to dissimilarity of aquatic insect fauna comparing to other lake districts (Table 23). Influence of these factors on the composition of aquatic fauna ought to be a subject of further detailed study.

**(iii) Biogeographic aspects** undoubtedly influence considerably the species richness of each European lake district. High species richness of the studied lakes can be, yet partially, explained by biogeographic features of this area. Since the biogeography of Bohemian Forest lakes insect is discussed above (see the chapter Biogeography), we emphasise only three crucial aspects showing an apparent influence on the large number of species living here. Contrary to other lake systems in Europe, the Bohemian Forest lakes are: (a) accessible (or a part of respective area) to species of all main types of “European” (Westpalaeartic) distribution (north- and south-central, central, Atlantic and Eurosiberian); (b) available from the southern (the Danube basin) as well as northern (the Elbe basin) natural ways of dispersal (biocorridors) of aquatic insects; and (c) enable co-existence of species with different faunistic origin (oreotundral, arboreal, or eremial), as well as different ecological requirements (at least cold stenothermic and eurythermic species).

**(iv) Climate conditions** (altitude, temperature, precipitation, ice and snow cover). An altitudinal gradient, closely connected with air/water temperature and the period of ice cover, represents one of the key factors influencing species richness of invertebrates and composition of assemblages in the mountain lakes. Ice cover, snow cover, and water temperature are controlled by the air temperature and thus climate is the main factor determining also species richness. In European alpine lakes, the average annual temperature decreases with elevation by 0.6–1.4°C per 100 m (LAJČZAK 1996, ŠPORKA et al. 2006) being, e.g., in the Tatra lakes, 1.6 and –3.8°C at the altitudes of 1778 and 2635 m a.s.l., respectively (KONČEK & ORLICZ 1974). Snow cover lasts from October to June, ice cover in the Tatra lakes increases with altitude at a mean rate of 10.2 days by every 100 m (CHOMITZ & ŠAMAJ 1974). Snow and ice cover directly or indirectly affects many of the physical chemical and biological processes

(cf. SMOL 1988) and, according to CATALAN et al. (2009), ice cover duration of 190 days represents a significant ecological threshold affecting lake biota.

These factors are responsible for a considerable decrease in species richness of aquatic insects with an increasing altitude nearly in all lake systems throughout the whole Europe discussed, moreover taking into account their much higher average altitudes (usually 1500–2500 m a.s.l., Table 22). HAMERLÍK et al. (2006) also observed an increase in abundance of non-insect fauna with increasing altitude. FÜREDER et al. (2006) described the highest species richness between 2400 and 2600 m a.s.l., but it decreased strongly above 2600 m in the Alps. DE MENDOSA & CATALAN (2010) considered similar altitude (2500 m a.s.l.) as an ecological threshold in the Pyrenees. This phenomenon can be explained by the ability of well-adapted species to use time-restricted input of food resources under extreme climatic conditions (cf. ČIAMPOROVÁ-ZAŤOVIČOVÁ et al. 2010). The altitudinal gradient is not so important in the Bohemian Forest lakes since the difference between the lowest and highest altitude is negligible (169 m, Table 1), although pronounced effects can be observed even along a short gradient (WHITEMAN 2000). Generally, their altitudes (918–1087 m a.s.l.) are lower than the majority of the lake districts under discussion, which are situated above the upper local tree line. The Bohemian Forest lakes differ from the majority of other lake districts discussed in relatively low altitude. Their location in coniferous forests results in a different input of allochthonous organic matter and different character of the lake littoral. They have lower precipitation compared to most remote alpine and subalpine lakes and a shorter snow cover (by at least 2 months; usually lasting from November to April). These conditions generally lead to a very high absolute number of species recorded in forest lakes, as shown by the comparison of species richness in lakes of forest, subalpine and alpine zones by HOFFMAN et al. (1996). They analyzed 88 taxa of macroinvertebrates in 41 oligotrophic lakes. About 86% of all taxa were recorded from forest zone lakes, 61% from subalpine zone lakes, and only 16% from alpine zone lakes. Consequently, only about 20% of the taxa are shared by forest and alpine lakes, which is very similar to the percentage of common taxa of the Bohemian Forest lakes and the alpine lakes throughout Europe (Table 22). Another consequence of lower altitude and altitude-related conditions is pronounced differences in assemblages of lakes (i.e. lentic habitat) and inlets/outlets (i.e. lotic habitat). In the Bohemian Forest lakes, there are about 30% of common taxa in inlets and outlets. This number is lower than indicated in the Alps (57%, MAIOLINI et al. 2006) and the Tatra Mts. (52%, HAMERLÍK et al. 2006). Likewise, inlets/outlets and lakes shared only about 20% species/taxa in the Bohemian Forest lakes comparing with 34% of common species/taxa in the Alps (BOGGERO & LENCIONI 2006). Lower contrast in composition of assemblages is probably caused by similar substrate and trophic conditions of habitats in the alpine zone (cf. HOFFMAN et al. 1996, BOGGERO & LENCIONI 2006, HAMERLÍK et al. 2006) when compared to the forest zone.

**(v) Fish stock** can play a crucial role in shaping macroinvertebrate assemblages in lakes and their impact could be stronger than the impact of acidification (MARCHETTO et al. 2004). Fish stock influences invertebrates directly by predation and indirectly by changes in trophic chains and food competition (KOWNACKI et al. 2000, DEMENDOZA & CATALAN 2010). Generally, lakes without or with only low densities of fish have more diversified and abundant invertebrate assemblages than those with higher fish densities (BENDELL & MCNICOL 1987, TATE & HERSHEY 2003, KERNAN et al. 2009c, SCHILLING et al. 2009). Favoured food sources for fishes in mountain lakes – mainly for trouts (*Salmo*, *Oncorhynchus*, *Salvelinus*), minnows (*Phoxinus*), or sculpins (*Cottus*) – are especially crustaceans (e.g., planktonic cladocerans and large branchiopods) and larvae of aquatic insects (e.g., mayflies, stoneflies, caddisflies, beetles, or chironomids) (CARLISLE & HAWKINS 1998, KOWNACKI et al. 2000, MARCHETTO et al. 2004). These taxa can show markedly lower diversity and often interrupted life cycles with

the occurrence of only small instars under stronger fish predation pressure (CUKER et al. 1992, KOWNACKI et al. 2000). Predaceous fish also eliminate large and predatory invertebrates and shift the assemblages toward smaller cryptic and less mobile taxa (BLOIS-HEULIN et al. 1990, CARLISLE & HAWKINS 1998). On the other hand, in the absence of fish, especially large, predatory and active swimming invertebrates are more diverse and abundant (NILSSON et al. 1994, RENNIE & JACKSON 2005, HEINO 2008, SCHILLING et al. 2009). In such cases, greater diversity and abundance of aquatic beetles, water bugs, dragonflies and some dipterans of the families Chironomidae and Chaoboridae occur and some representatives of these taxa even can be used as indicators of fish absence (NILSSON et al. 1994, BENDELL & MCNICOL 1987, SCHILLING et al. 2009).

From this point of view, high invertebrate species richness in the Bohemian Forest lakes can also be a result of co-influence of their relatively lower altitude compared to more frequently studied alpine lakes and the absence of fish in the last 50 years as a result of strong acidification (VRBA et al. 2003a). Yet a population of brook trout (*Salvelinus fontinalis*) has been quite recently proven by electro-fishing in Kleiner Arbersee (W. DÖRFER, pers. com.). If there is fish recovery in the studied lakes, one should expect a decrease in both abundance and diversity of invertebrates in the subsequent years (RASK et al. 2001). We can expect, however, that the impact of fish predation under natural conditions on biomass of invertebrate prey is generally weak in littoral habitats compared to the open profundal zone, owing to more structurally complex environment in the littoral serving as a refuge for invertebrates (PIERCE & HINRICHS 1997, BOGGERO & LENCIONI 2006, NASMITH et al. 2012). Indeed, the littoral zones with macrophyte beds in the Bohemian Forest lakes provide excellent habitats for most of the recorded aquatic insect taxa.

**(vi) Sampling techniques and sample processing.** There is no doubt that species richness cannot be studied without employing appropriate sampling techniques, otherwise some species (or groups) would escape our attention and the results would be strongly underestimated. There is no necessity to discuss special techniques used in our study here in detail since their applications have been mentioned in special chapters dealing with individual groups or in the Material and methods. We believe that combination of several sampling techniques appropriate for collecting of insects of various life strategies might describe species richness of lakes much more accurately than some routine standardized sampling.

Some studies (e.g., KRNO 1991, FÜREDER et al. 2006, ČIAMPOROVÁ-ZAŤOVIČOVÁ et al. 2010, ČIAMPOROVÁ-ZAŤOVIČOVÁ 2011) are based on quantitative sampling with a Surber or Hess samplers, which is not able to sample representatively pleustonic and actively swimming species and species with low population densities. Thus most Odonata, Heteroptera, Coleoptera, and Diptera other than Chironomidae are often missing in their samples. Such a bias can be prevented by parallel sampling with a hand net that enable better detection of actively moving specimens compared to sampling of the framed bottom area (SYCHRA & ADÁMEK 2010) and/or selective sampling of actively swimming species (e.g., traps and individual collecting by a strainer).

Time limited semiquantitative kick samples collected by a hand net with mesh size of 250–500  $\mu\text{m}$  according to FJELLHEIM et al. (2000) were used in the majority of studies taken for comparison (KOWNACKI et al. 2000, OERTLI et al. 2008, BOGGERO & LENCIONI 2006, KRNO 2006, KRNO et al. 2006, FJELLHEIM et al. 2009, KERNAN 2009a, DE MENDOSA & CATALAN 2010). Different (but not group-specialized) sampling techniques have been used only exceptionally. For instance, KOWNACKI et al. (2000) used a corer to sample muddy substrata and KRNO (2006) used yellow Moericke traps for collecting imagines of aquatic insects. In our study, we have employed semiquantitative sampling by a hand net to determine the composition of assemblages supplemented by different group-specific sampling techniques (such as indivi-

dual collecting by a metal strainer, light trapping, pupal exuviae collecting, and sweeping of imagines). This could considerably favour the total number of species recorded to number of species detected by the only standardised method.

Both timing and frequency of sampling largely affect the final species richness. In the Bohemian Forest lakes, we sampled each lake in late spring (from mid May to early June), full summer (August), occasionally just after ice melting (late April) and in autumn (late September or October). Such timing is the only way to detect all species of different life cycles. In fact, only semivoltine (some dragonflies and alderflies) and polyvoltine (some Diptera) species can be reliably detected when applying one-shot sampling; however, they seldom dominate the assemblages. The detection of univoltine species, i.e. the majority of aquatic insects, is more tangled due to different timing and growth rate of species. When applying one-shot sampling, many species may be in the life-stage not allowing proper determination to the species level, or not detectable at all. Unfortunately, most authors based their results on a single sample per ice-free season (KOWNACKI et al. 2000, OERTLI et al. 2008, BOGGERO & LENCIONI 2006, FÜREDER et al. 2006, KRNO 2006, KRNO et al. 2006, HEINO 2008, FJELLHEIM et al. 2009, KERNAN 2009a, DE MENDOSA & CATALAN 2010). Hence, their approach can hardly cover entire species diversity of aquatic insect and might be the cause of incomparable species richness found in the Bohemian Forest lakes. Also ČIAMPOROVÁ-ZAŤOVIČOVÁ et al. (2010) and ČIAMPOROVÁ-ZAŤOVIČOVÁ (2011) who applied far more frequent sampling (8–13 times at each lake) found species richness as high as 81 species in four lakes. In contrast, KRNO et al. (2006) collected only 79 species by one-shot sampling of 45 (!) lakes in the same area (including the above-mentioned 4 lakes).

The other factor, which can strongly affect comparability of results, is the determination level of the collected specimens. In our study, imagines were collected, because, for many species (e.g., Diptera and Plecoptera), they were the only life stage identifiable to species level. Therefore, the diversity of these groups is often roughly underestimated. Many studies are based on determinations on the genus or even family level, which hide considerable part of species richness. Large-scale studies usually use harmonised data (cf. FJELLHEIM et al. 2009, KERNAN et al. 2009b) that enable objective statistical analysis, however, such data are not very useful to determine or compare exact species richness.

### **Species (taxa) diversity of individual groups investigated**

#### **Ephemeroptera**

The Bohemian Forest lakes exhibited the same number of mayfly species/taxa (altogether 9 species inhabit the lake littoral, Table 23) as in the Fennoscandian lakes, where the highest number of mayfly species of all districts were recorded. High species richness (8 taxa) was observed in Scottish lakes. Six genera were mentioned from the Pyrenees, and five and four species were recorded in the Tatra Mts. and the Alps, respectively. On the contrary, no Ephemeroptera were found in the Retezat Mts. in Romania, and only one species was found in the Rila Mts. in Bulgaria.

In all European lakes districts investigated, there are approximately 14 species (taxa) that have never been found in the Bohemian Forest lakes including their inlets/outlets, although most of them are common in the Czech Republic and Germany. They comprise (i) lowland and colline species occurring in the lakes of low altitudes (*Centroptilum luteolum*, *Paraleptophlebia* sp., *Caenis horaria*); (ii) lowland and colline rather potamal species, most likely only incidentally found in mountain lakes or their inlets/outlets (*Ecdyonurus aurantiacus*, *Heptagenia* sp., *Caenis luctuosa*); (iii) submontane and montane species, the area of which does not comprise the Bohemian Forest, like species distributed only or predominantly in

**Table 23.** Numbers of identical taxa of seven selected lake districts investigated throughout Europe in 1991–2011 compared with species/taxa diversity of the eight Bohemian Forest lakes (only taxa living in the lake littoral considered, i.e. 196 taxa); Abbreviations: EPH – Ephemeroptera (9 species in the Bohemian Forest lakes), ODO – Odonata (19 species in the Bohemian Forest lakes), PLE – Plecoptera (7 spp.), HET – Heteroptera (32 spp.), MEG – Megaloptera (2 spp. + 1 sp. of aquatic Neuroptera), TRI – Trichoptera (19 spp.), COL – Coleoptera (49 spp.), CHI – Diptera, Chironomidae (47 taxa in the Bohemian Forest lakes), DIP – other families of Diptera. See Table 22 for total number of identical species (taxa) found.

Reference/Order (number of taxa in the studied lakes)	EPH (9)	ODO (19)	PLE (7)	HET (32)	MEG (2)	TRI (19)	COL (49)	CHI (47)	DIP (12)	Note
HEINO (2008)	3	2	1	2	1	6	4	6	0	DIP not found
BRODERSEN et al. (1998)	2	2	2	2	1+1	6	1	9	1	<i>Sisyra</i> sp. found
KERNAN et al. (2009)	3	0	3	1	1	9	1	22	1	ODO not found
KOWNACKI et al. (2000)	0	0	1	0	0	1	2	12	0	ODO, EPH, HET, MEG, DIP not found
KRNO (2006), KRNO et al. (2006)	1	0	5	0	1	2	9	15	0	ODO, MEG not found
ČIAMPOROVÁ-ZAŤOVIČOVÁ et al. (2010), ČIAMPOROVÁ-ZAŤOVIČOVÁ (2011)	2	0	1	0	0	1	2	7	0	ODO not found
MARCHETTO et al. (2009)	–	–	–	–	–	–	–	10	–	only CHI considered
FÜREDER et al. (2006)	2	2	4	1	2	5	4	10	5	
BOGGERO & LENCIONI (2006)	6	2	5	2	0	2	2	17	2	MEG not found
OERTLI et al. (2008)	0	0	1	1	0	1	4	8	3	EPH, ODO, MEG not found; DIP determined into families
DE MENDOSA & CAVALAN (2010)	2	2	3	1	1	3	4	17	1	taxa determined at family/genus level only
FJELLHEIM et al. (2009) Central Norway	1	0	3	1	0	3	2	10	1	ODO and MEG not found; HET indet.
FJELLHEIM et al. (2009) Italian Alps	0	0	2	1	0	1	2	7	1	EPH, ODO, MEG not found; HET indet.
FJELLHEIM et al. (2009) Julian Alps, Slovenia	1	0	1	1	0	1	2	6	0	ODO, MEG, and DIP not found; HET indet.
FJELLHEIM et al. (2009) Polish Tatras	0	0	3	0	0	0	0	7	0	EPH, ODO, HET, MEG, TRI, and COL not found
FJELLHEIM et al. (2009) Slovakian Tatras	0	0	1	0	0	0	2	6	1	ODO, EPH, HET, and MEG not found
FJELLHEIM et al. (2009) Retezat Mts. Romania	0	0	0	0	0	1	0?	3	0	EPH, ODO, PLE, HET, MEG, and DIP not found
FJELLHEIM et al. (2009) Rila Mts., Bulgaria	1	0	3	1	1	1	1	1	0	ODO not found; HET indet.

the Alps (*Rhithrogena* gr. *hybrida*, *Ecdyonurus* gr. *helveticus*, *Epeorus alpicola*); and (iv) colline or submontane species reaching lakes and their inlets/outlets only in high mountains in the Tatra Mts. or the Pyrenees (*Baetis niger*, *Electrogena lateralis*, *Rhithrogena semicolorata*, *Cloeon simile*, *Ephemera vulgata*).

In the Fennoscandian and Danish lakes situated at relatively low altitude, some lowland and colline species of mayflies do occur, contrary to the Bohemian Forest lakes. Apart from the genera *Cloeon*, *Leptophlebia*, and *Baetis* living in the Bohemian Forest as well, HEINO (2008) collected some species of the genera *Heptagenia*, *Caenis*, and *Ephemera* in the lakes of the Oulankajoki in Finland. These genera do not occur in the Bohemian Forest lakes. Most species showed high frequency of occurrence (in 45–47 lakes out of 48 lakes investigated), species of *Heptagenia* was collected only in 15 lakes. Similarly, BRODERSEN et al. (1998) found larvae of *Centroptilum luteolum*, *Ephemera vulgata*, *Caenis horaria*, and *C. luctuosa* in Denmark. Only two taxa, *Cloeon* spp. and *Leptophlebia marginata*, were common with the Bohemian Forest lakes. FJELLHEIM et al. (2009) collected *Siphonurus lacustris* and *Ecdyonurus* sp. in central Norway in addition to unusual finding of *Cloeon simile*, a colline species not occurring in the Bohemian Forest.

In Scotland, the following species were found in the lake littoral: *Ameletus inopinatus*, *Baetis muticus*, *B. niger*, *B. rhodani*, *Baetis* spp., *Heptagenia* sp., *Leptophlebia* sp., and *Paraleptophlebia* sp. (KERNAN et al. 2009a). These mayflies, except for *Ameletus* and *Leptophlebia*, do not inhabit standing waters in the Czech Republic. Their habitat preferences are most probably a little different in Scotland, which was observed in Plecoptera as well (see the chapter Stoneflies below).

In the Pyrenees, DE MENDOSA & CATALAN (2010) observed 6 mayfly genera (species not determined): *Siphonurus*, *Cloeon* (sub *Cloëon*), *Ecdyonurus*, *Electrogena*, *Habroleptoides*, and *Caenis*. There is a little doubt whether the taxon “*Cloëon*” does not in fact represent the genus *Baetis*. It is the most frequent (collected in 19 of 82 lakes) and the most abundant mayfly. Larvae were collected mostly at altitudes of 2100–2300 m a.s.l.

Lakes in the Alps are relatively poor in the occurrence of mayflies. All the authors found only 2 taxa of mayflies. FÜREDER et al. (2006) collected *Siphonurus lacustris* (only in 1 site) and *Baetis* sp.; BOGGERO & LENCIONI (2006) collected *S. lacustris* and *Baetis alpinus*, and FJELLHEIM et al. (2009) found two taxa as well, *S. lacustris* and *Ecdyonurus* sp.

No representatives of the mayflies were collected either in Polish or Slovak lakes of the Tatra Mts. according to KOWNACKI et al. (2000) and FJELLHEIM et al. (2009). This was definitely not realistic, because other authors mentioned five species from the Tatra lakes (Table 22): *Ameletus inopinatus*, *Baetis alpinus*, *Baetis vernus*, *Electrogena lateralis*, and *Rhithrogena loyolaea*.

As far as we know, the name *Rhithrogena loyolaea carpathica* used by KRNO et al. (2010) most probably represents an undesirable *nomen nudum* and the problem of possibly polytypic *Rh. loyolaea* definitively must not be treated or solved in such a way (cf. ICZN 1999) since the taxon of *Rh. loyolaea* populations from the High Tatra Mts. has been named many years ago by ZELINKA (1953). He named and described *Rhithrogena tatica* Zelinka, 1953 from the type locality, the Mlynica stream near Štrbské Pleso. The holotype (♂ imago) and paratypes were originally deposited in the Masaryk University in Brno, Czech Republic (present whereabouts unknown, probably lost, cf. BAUERNFEIND & SOLDÁN 2012). Later, THOMAS (1970) synonymised the Zelinka's species with *Rh. loyolaea* Navás, 1922 described from the Iberian Peninsula (Spain) and widely distributed in the Pyrenees, the Alps, and most Hercynian mountains in Europe. On the contrary, TOMKA & RASCH (1993) considered *Rh. tatica* and *Rh. loyolaea* to represent the different species and removed *Rh. tatica* from the synonymy with *Rh. loyolaea* (diagnostic characters used, however, are demonstrably vari-

able at least in some populations). Studying numerous populations from different European mountains in details, KLONOWSKA-OLEJNIK & GODUNKO (2003) recognised a Carpathian population and an Alpine population within *R. loyolaea*, differing in larval characters but not separable in male imagines. The taxonomic situation is, however, still far from clear. Specimens from the Eastern Alps (Austria) and the Hercynian mountain system including the specimens from the Bohemian Forest lakes (Czech Republic) are somewhat intermediate in larval characters, suggesting a clinal change from east to west. Probably the status of *Rhithrogena tatrlica* Zelinka, 1953 should be re-evaluated for the Carpathian populations with regards to establishment of a new subspecies as suggested by KRNO et al. (2010).

*Leptophlebia vespertina*, the most frequent and abundant species of mayflies in the Bohemian Forest lakes, exhibits a remarkable disproportion in its distribution in other European lake systems. Larvae have not been collected in lakes either in the Alps, in the Pyrenees, or in the Carpathians in Romania and other Balkan mountains (FJELLHEIM et al. 2009). The species was recorded from Scandinavia (e.g. BRITAIN 1974, 1978, 1980), although recently not detected by FJELLHEIM et al. (2009) in central Norway, and possibly also in lakes in Scotland, as *Leptophlebia* sp. (KERNAN et al. 2009a). The species was known from lakes in the High Tatra Mts. (SCHOENEMUND 1930a, HRABĚ 1942, LANDA 1969, KRNO 1988, 1991). However, the last record (but without any concrete data) in the Tatra lakes was published by KRNO et al. (2010) quoting *L. vespertina* abundant in all dystrophic lakes at lower altitudes. Larvae apparently disappeared from some lakes in this area recently (KRNO 2006, KRNO et al. 2006, HAMERLIK et al. 2006, ČIAMPOROVÁ-ZAŤOVIČOVÁ et al. 2010, ČIAMPOROVÁ-ZAŤOVIČOVÁ 2011), at least from the lakes above 1500 m a.s.l. While LANDA & SOLDÁN (1989) observed mass occurrence of larvae both in Štrbské Pleso (1343 m a.s.l.) and Jamské Pleso (1447 m a.s.l.) lakes, we failed to find any larvae at least in the former lake in 2010 (SOLDÁN & BOJKOVÁ, unpubl. data), which might be caused by some physico-chemical impact, undoubtedly other than acidification.

In contrast, *Siphonurus lacustris* suggested an increase in abundance of larvae in some low-altitude (forest) lakes in the Tatra Mts. (KRNO et al. 2010). Such quantitative changes have never been observed in the Bohemian Forest lakes, where both dominating species (*S. lacustris* and *L. vespertina*) show certain equilibrium in their population dynamics development due to their different fitness and highly adapted life cycle strategies (BRITAIN 1978, SÆTTEM & BRITAIN 1993, this study – chapter Mayflies). A similar phenomenon has been observed in mountain reservoirs shortly after their impoundment in some Hercynian mountains in Bohemia (SOLDÁN et al. 1998, SOLDÁN & ZAHŘÁDKOVÁ 2000). At these places, larvae of *S. lacustris* are able to occupy a newly established niche, contrary to other mayfly species living at the same habitat, including *Leptophlebia* species. Obviously a different factor affected quantitative increase of larvae of *S. lacustris* in some Tatra lakes mentioned by KRNO et al. (2010), since no new niches were formed there. These changes could be connected with a decrease in or even disappearance of larvae of *L. vespertina* mentioned above but the proper mechanism remains still unknown.

## Odonata

The number of Odonata collected in the Bohemian Forest lakes (at least 19 species) seems to be extremely high in comparison with literature data on dragonfly presence in lakes or lake districts throughout Europe. Odonata, together with Heteroptera and Diptera except Chironomidae, belongs to the most neglected insect groups in European lakes in general. For instance, FJELLHEIM et al. (2009) did not find any specimens in 7 lake districts in Europe, KERNAN et al. (2009a) did not detect dragonflies in Scotland, neither did several authors in the Tatra Mts. (KOWNACKI et al. 2000, KRNO et al. 2006, ČIAMPOROVÁ-ZAŤOVIČOVÁ 2011), nor

in some parts of the Alps (OERTLI et al. 2008, Table 23). Dragonflies escaped the attention due to their high vagility and obviously temporary occurrence in some lakes; moreover, their larvae, as top predators, often showed low densities in comparison with other groups.

Most records were based on at most several (usually 2–5) species, often without proper determination. HEINO (2008) referred on the occurrence of *Coenagrion* sp., *Aeshna* sp., and *Somatochlora* sp. in Finish lakes. BRODERSEN et al. (1998) even operated with units such as “Coenagrionidae” or “Zygoptera” when studying macroinvertebrates in Danish lakes.

Remarkable findings are those by FÜREDER et al. (2006) who studied 55 lakes across three regions of the Alps in Italy, Switzerland, and Tyrol in Austria. He noticed a rare occurrence of three species in the littoral of a few lakes. While the species of the genera *Aeshna* and *Orthetrum* usually cannot be identified, the authors determined two more species, namely *Aeshna cyanea* (the most abundant dragonfly in our lakes) and *Anaciaeschna isosceles* (Müller, 1761) (sub *Aeshna isosceles* Müller, 1761). The occurrence of the latter species seems to be incidental (reproduction quite unlikely) since it prefers much lower altitude than an altitudinal range of 1840–2796 m a.s.l. studied by FÜREDER et al. (2006). While in the Czech Republic the species prefers the elevations of 130–399 m a.s.l. (highest altitude 625 m), the range of 100–830 m a.s.l. is preferred in Austria (DOLNÝ et al. 2007). In the Czech Republic, the species is stenotopic, developing in meso- and eutrophic warmed waters (including artificial ones) overgrown with aquatic plants.

From the Pyrenees, two genera of Odonata are recorded: *Aeshna* and *Enallagma*, five findings in 82 lakes investigated (DE MENDOSA & CATALAN 2010). While the representative of the genus *Aeshna* cannot be identified without a revision of the original material, the latter species most probably represent *Enallagma cyathigerum* since no more representative of the genus from Europe is known (cf. ASKEW 1988). Odonata were collected at the considerable altitudes of 1900–2200 m a.s.l.

The occurrence of dragonflies in the Tatra lakes seems to be a little controversial. There are no data on any species sampled in about 50 lakes in the Tatra Mts. recently investigated in Slovakia (KRNO 2006, KRNO et al. 2006, FJELLHEIM et al. 2009, ČIAMPOROVÁ-ZAŤOVIČOVÁ et al. 2010, ČIAMPOROVÁ-ZAŤOVIČOVÁ 2011) and Poland (KOWNACKI et al. 2000). Only KRNO (1991) reported four species (*Pyrrhosoma nymphula*, *Aeshna subarctica*, *Ae. juncea*, and *Somatochlora metallica*), known also from the Bohemian Forest lakes.

In contrast, using qualitative entomological methods (collecting of imagines), as much as 15 species were found at the single lake, Štrbské Pleso: *Lestes sponsa*, *Pyrrhosoma nymphula*, *Enallagma cyathigerum*, *Coenagrion hastulatum*, *C. puella*, *Ischnura pumilio*, *Aeshna caerulea*, *Ae. cyanea*, *Ae. juncea*, *Ae. subarctica*, *Somatochlora alpestris*, *S. arctica*, *S. metallica*, *Sympetrum danae*, and *Leucorrhinia dubia* (TRPIŠ 1965, STRAKA 1990). Naturally, some species could be occasional visitors or migrating specimens, but there is no doubt that the majority of species (e.g., *Lestes sponsa*, *Enallagma cyathigerum*, *Coenagrion puella*, *Aeshna cyanea*, *Somatochlora metallica*, *Leucorrhinia dubia*) can reproduce at least in the lakes at lower altitudes (for details, see DAVID 2001, 2005, ŠACHA 2006). This is an example of how standard hydrobiological methods can fail in detecting species diversity, which could also happen in other lake districts.

The species composition roughly fits to a dragonfly taxocene of the Bohemian Forest lakes, except for the absence of *Somatochlora alpestris* and *S. arctica* that can be supposed to occur in the Bohemian Forest lakes. However, there is one more species reported from the Tatra lakes (STRAKA 1990) that was not collected in the Bohemian Forest lakes: *Sympetrum vulgatum*. It is a lowland, eurytopic species not distributed in the Bohemian Forest (96% of localities in the Czech Republic are at the altitudes of 130–599 m a.s.l.; HANEL & ZELENÝ 2000, DOLNÝ et al. 2007) and its occurrence in the Tatra lakes is probably incidental, althou-

gh the localities at 1350 m a.s.l. are recorded from the Krkonoše (Giant) Mts. (DOLNÝ et al. 2007). Only five species (*Ischnura elegans*, *Cordulia aenea*, *Libellula quadrimaculata*, *Orithetrum cancellatum*, *Sympetrum sanguineum*) collected in the Bohemian Forest lakes were not found in the Tatra lakes.

## Plecoptera

Considering seven species found at present in the Bohemian Forest lakes, the species diversity of Plecoptera known from the lake districts across Europe is comparable. The Tatra lakes are the only exception, because they are inhabited by 16 stonefly species. High species richness was found in the Alpine (7 species) and Scottish lakes (11 species). In contrast, no Plecoptera were collected in the Retezat lakes in Romania or in high alpine ponds in Switzerland.

However, some authors left Plecoptera determined only at the generic or even family level, so that their data are not comparable with ours. It concerns mainly lakes in Fennoscandia and the Pyrenees. FJELLHEIM et al. (2009) reported, besides “Plecoptera indet.,” larvae of *Nemurella pictetii* and five further unidentified genera (*Diura* sp., *Isoperla* sp., *Nemoura* sp., *Capnia* sp., *Leuctra* sp.) and HEINO (2008) mentioned the only genus *Nemoura* from Finland. DE MENDOSA & CATALAN (2010) found six genera of stoneflies (*Arcynopteryx*, *Perlodes*, *Nemoura*, *Nemurella*, *Capnia*, and *Leuctra*) in the Pyrenees, which were very rare. These studies probably undervalued the diversity of lake stoneflies in these regions. For example in Fennoscandia, no fewer than 17 species are known to occur in lakes (LILLEHAMMER 1985).

Seven species were found in the Alpine lake district (BOGGERO & LENCIONI 2006, FÜEREDER et al. 2006, FJELLHEIM et al. 2009). They were collected rather occasionally (cf. FÜEREDER et al. 2006) and some of them were identified only to the genus level (*Perlodes* sp., *Nemoura* sp., *Protonemura* sp., and *Leuctra* sp.). Two species were identical with those found in the Bohemian Forest lakes (*Nemoura cinerea* and *Nemurella pictetii*), while one species was different – *Dictiogenus fontium* is an Alpine species, not distributed in the Czech Republic.

High species richness of stoneflies was found by KERNAN et al. (2009a) in Scotland, altogether 11 species/taxa have been found. Besides species living also in the Bohemian Forest lakes (*Nemoura cinerea*, *Nemurella pictetii*) or their inlets/outlets (*Diura bicaudata*, *Amphinemura sulcicollis*, *Leuctra hippopus*, *Protonemura montana*, *Siphonoperla torrentium*), two other species have been collected (*Capnia atra*, *Dinocras cephalotes*); yet the former does not occur in the Czech Republic. Remaining species were left unidentified (*Capnia* sp., *Nemoura* sp.).

The Tatra lakes exhibited the highest number of lake Plecoptera across the European lake districts. Sixteen species were found in the Tatra lakes (KRNO et al. 2006, ČIAMPOROVÁ-ZATOVÍČOVÁ 2011). Only four of them are common with the Bohemian Forest lakes: *Nemoura cinerea*, *Nemurella pictetii*, *Leuctra nigra*, and *L. pusilla*. Some other species (*Diura bicaudata*, *Amphinemura standfussi*, *Capnia vidua*, and *Leuctra pseudosignifera*) were found only in inlets and outlets of our lakes. The remaining species, except *Arcynopteryx compacta* found in the Pyrenees and *Dinocras cephalotes* found in Scotland, are unique in the Tatra lakes, because they were not recorded in any other lake district: *Isoperla sudetica*, *Siphonoperla neglecta*, *Protonemura brevistyla*, *P. nimborum*, *Leuctra armata*, and *L. rosinae*.

Apart from the obvious absence of many Alpine and Carpathian montane species, the main difference of stoneflies of the Bohemian Forest lakes compared to other European lake districts is caused by different habitat preference of species in different lake districts. Several species known from European lakes have never been collected in lakes or other standing water habitat in the Czech Republic and are exclusive inhabitants of running waters. Moreover, these species were often found in inlets and outlets of the Bohemian Forest lakes. For

instance, *Dinocras cephalotes*, *Diura bicaudata*, *Capnia vidua*, and *Leuctra pseudosignifera*, known from the Tatra lakes, *D. bicaudata*, *Siphonoperla torrentium*, *Amphinemura sulcicollis*, *Protonemura montana*, and *Leuctra hippopus*, known from Scottish lakes, and several species, such as *Amphinemura standfussi*, *Protonemura meyeri*, and *Leuctra fusca*, known from Fennoscandinavian lakes (LILLEHAMMER 1985). It could be caused by different character of the littoral and temperature of the Bohemian Forest lakes. Many high-altitude lakes have the stony littoral, which is similar to bottom of running waters and/or adjacent sections of inlets and outlets. Our lakes have developed vegetation or abundant organic substrate in the littoral, which can be unfavourable to running water stoneflies. At the same time, the number of running water stoneflies able to inhabit lakes increases with latitude. Many strict inhabitants of small streams occur in lakes in Great Britain and Fennoscandia (cf. LILLEHAMMER 1985, 1988, HYNES 1984), which could be connected with different temperature regime of lakes.

## Heteroptera

Similarly to Odonata, Heteroptera of the European lakes seem to be rather overlooked and only marginal attention has been devoted to this group by authors studying benthic assemblages of the lakes across Europe (Table 22). The representatives of Heteroptera often apparently escape the attention owing to their relatively high vagility and migratory behaviour. Moreover, some species prefer to live in open water or on the water surface, thus, can be hardly detected by routine and usual sampling techniques. This group is a typical example, the sampling of which requires specialised techniques from individual collecting by specialist to light traps. Data presented below would indicate nearly total absence of Heteroptera in the European lakes in general. We believe that careful entomological research of these habitats would display species diversity comparable with the Bohemian Forest lakes.

Representatives of the families Nepidae, Notonectidae, Naucoridae, and Pleidae collected in the Bohemian Forest lakes have not been recorded yet from the European mountain glacial lakes chosen for comparison. Most authors, moreover, seems to be satisfied with a determination at the family level or even higher level. For instance, FJELLHEIM et al. (2009) found Heteroptera in four of lake districts across Europe (central Norway, the Italian Alps, the Julian Alps, and the Rila Mts.) but they left this group as “Heteroptera indet.”

Two families of Heteroptera were found in European lakes in the studies selected for comparison with our lakes. Of the family Micronectidae, only *Micronecta* sp. was found in Denmark (BRODERSEN et al. 1998) and the Pyrenees (DE MENDOSA & CATALAN 2010). In our lakes, *Micronecta scholtzi* has been found in one lake (Table 9). Of the species-rich family Corixidae, only *Sigara* sp. was found in Finland (HEINO 2008), Corixinae in Denmark (BRODERSEN et al. 1998) and unidentified Corixidae in Scotland (KERNAN et al. 2009a). *Arctocoris carinata carinata* is the only species widely distributed across the European mountain lakes that was not detected in the Bohemian Forest lakes. Predominantly predaceous *A. carinata* is vagile boreo-alpine species with Palaearctic disjunctive distribution. A centre of its distribution lies in northern Europe (JANSSON 1986). The species has been infrequently collected in the Pyrenees (as *Arctocoris* sp., de MENDOSA & CATALAN 2010), some lakes and outlets of the Alps (BOGGERO & LENCIONI 2006, FÜREDER et al. 2006, NIESER 1981, OERLI et al. 2008) and lakes in the Tatra Mts. (KRNO 1991, KLEMENTOVÁ 2012). The historical record of the species from glacial lakes in the Slovakian part of the Tatra Mts. mentioned by ŠTUSÁK (1980) was based on imperfect translation of SZILÁDY (1904). Contemporary studies of the Tatra lakes (KOWNACKI et al. 2000, KRNO 2006, KRNO et al. 2006, FJELLHEIM et al. 2009, ČIAMPOROVÁ-ZAŤOVIČOVÁ et al. 2010, ČIAMPOROVÁ-ZAŤOVIČOVÁ 2011) did not mention any Heteroptera. *A. carinata* occurs in lakes located in mountain meadows or peatbogs (cf. NIESER

1981, WACHMANN et al. 2006), as well as in rock pools (PAJUNEN & PAJUNEN 1992, 1993). NIESER (1981) found this species in Northern Tyrol (peat pond with an area of ~1 ha, 1300 m a.s.l.). ŠTYS (1976) analyzed the food of brook trout from the Fláje reservoir (ca. 153 ha, 737 m. a.s.l., Krušné Hory Mts., Czech Republic) and found this species (2 ♀♀) in the fish stomachs. Hence, presence of *A. carinata* in the fishless Bohemian Forest lakes is likely.

Based on the studies selected for comparison, any other taxa of the family Corixidae, i.e., the genera *Cymatia* (*C. bonsdorffii*), *Glaenocorisa* (*G. propinqua*), *Callicorixa* (*C. praeusta*), *Corixa* (*C. punctata*), *Hesperocorixa* (*H. sahlbergi*), *Paracorixa* (*P. concinna*), and *Sigara* in 4 subgenera (*Pseudovermicorixa*, *Retrocorixa*, *Subsigara*, *Vermicorixa*; Table 9) have not been reported from any other lake district besides the Bohemian Forest. NIESER (1981), however, studied life cycles of water bugs in ponds and smaller water bodies in the Tyrolean Alps and found similar water bugs taxocenoses as we recorded from the Bohemian Forest lakes. Therefore, one can expect a similar spectrum of water bug species in other (at least central) European mountain oligo- to mesotrophic lakes, as well.

To conclude, the present fauna of Heteroptera (altogether 32 of Nepomorpha and Gerromorpha species) of the Bohemian Forest lakes seems to be quite unique within the European mountain glacial lakes chosen for comparison, considerably richer than in any other lake district. However, as emphasised above, the negative records are, in a great extent, due to overlooking this insect group rather than their “true” absence. Besides considerably scarce records of most species currently occurring in the Bohemian Forest lakes, the most remarkable difference is the absence of *Arctocorisa carinata*, a species otherwise widely distributed in European mountain lakes, in this area.

#### Megaloptera and aquatic Neuroptera

Megaloptera are represented by the only family Sialidae and the only genus *Sialis* in European lakes. *Sialis fuliginosa* has been found frequently in inlets/outlets of the Bohemian Forest lakes, while larvae live only in two lakes. Within all other European lakes studied this species (like any other species of *Sialis*) has not yet been found except for some lakes in the Alps. Although larvae of this species are known to prefer waters of rather lower altitudes, FÜREDER et al. (2006) reported the larva (sub *Sialis* cf. *fuliginosa*) from the elevations of at least 1840 m a.s.l. However, other authors did not find any Megaloptera in the Alpine lakes (Table 22).

Any other records on the occurrence of Sialidae or *Sialis* sp. most probably concern the species of *S. lutaria*. The species was found in lakes in Finland and Denmark (HEINO 2008, BRODERSEN et al. 1998). KERNAN et al. (2009a) reported Sialidae (without further genus/species determination) from some lakes in Scotland and DE MENDOSA & CATALAN (2010) reported *Sialis* sp. from the Pyrenees, where larvae were mostly found at high altitude (2100–2300 m, occasionally over 2500 m) in relatively high densities. *S. lutaria* was found also in the Tatra lakes in Slovakia (KRNO et al. 2006, ČIAMPOROVÁ-ZAŤOVIČOVÁ 2011), where it inhabited strongly acidified lakes with high concentration of phosphorus and amount of particulate organic matter in the littoral (KRNO et al. 2006), while Megaloptera have not been found in the Tatra lakes in Poland (KOWNACKI et al. 2000, FJELLHEIM et al. 2009).

As far as we know the only mention of aquatic Neuroptera in literature is that by BRODERSEN et al. (1998), who found *Sisyra* sp. in the single lake in Denmark. Otherwise the aquatic Neuroptera have not yet been mentioned from any European lake district.

#### Trichoptera

There is no doubt that caddisflies, contrary to Odonata, Heteroptera and partly Coleoptera, have received an appropriate attention in studies of species diversity of the European lake

systems. Despite some difficulties in determination of larvae of some groups (e.g., the family Limnephilidae), most species can be used, besides the Chironomidae, also as “flagship indicators” in the assessment of acidification and climatic changes in mountains (cf. ČIAMPOROVÁ-ZAŤOVIČOVÁ et al. 2010).

At present, the richest Trichoptera taxocenoses has been found in the Slovak Tatra lakes (28 species; KRNO 1991, CHVOJKA 1992). Data from other European lake districts are based on larval identifications and total numbers could be underestimated – e.g., 16 species/taxa (including unidentified Limnephilidae and Polycentropidae) were reported from Scotland (KERNAN et al. 2009a), 14 species from the Alpine lakes (BOGGERO & LENCIONI 2006, FÜREDER et al. 2006, OERTLI et al. 2008), and 24 taxa from lowland Danish lakes (BRODERSEN et al. 1998; Table 23). The species diversity of caddisflies of the Bohemian Forest lakes (19 species) is roughly comparable with these European lake districts.

The Bohemian Forest lakes are similar in the species composition of caddisfly taxocenoses to those in the montane zone in the Slovak part of the Tatra Mts. Ten species, namely *Polycentropus flavomaculatus*, *Holocentropus dubius*, *Cyrnus flavidus*, *C. trimaculatus*, *Oligotricha striata*, *Phryganea bipunctata*, *Limnephilus coenosus*, *L. rhombicus*, *Molannodes tinctus*, and *Mystacides azurea* (KRNO 1991, CHVOJKA 1992), are common for both groups of lakes. Most of the species inhabiting the Bohemian Forest lakes were eurytopic species, which can be found not only in various types of standing waters at different altitudes and also in (slow) flowing waters. Some of these species (*Polycentropus flavomaculatus*, *Cyrnus flavidus*, *C. trimaculatus*) were also found in the lowland lake district in Denmark (BRODERSEN et al. 1998). Species *Plectrocnemia conspersa*, *Polycentropus flavomaculatus*, *Mystacides azurea*, and *Chaetopteryx villosa* are common in the Scottish lake district (KERNAN et al. 2009a), while *Plectrocnemia conspersa*, *Polycentropus flavomaculatus*, *Oligotricha striata*, and *Limnephilus coenosus* are frequent in Alpine lakes of high altitude in Italy, Switzerland, and Austria (BOGGERO & LENCIONI 2006, FÜREDER et al. 2006, OERTLI et al. 2008).

## Coleoptera

As high species diversity of Coleoptera in the Bohemian Forest lakes (55 species, 49 of them living permanently in the lakes at present) suggests, the representatives of this group are largely underestimated or overlooked. This is due to a lesser attention paid to aquatic beetles and using of inadequate sampling methods for collecting of all present beetle taxa (cf. LANDIN 1976a) rather than difficulties in species determination. Nevertheless, some authors leave this taxon undetermined (usually like “Coleoptera indet.”), some others rely on a determination only at the family or generic levels so that our knowledge of aquatic beetles in some lake systems (e.g., in Scotland, Norway or Balkans) remains very fragmentary (cf. KERNAN et al. 2009a or FJELLHEIM et al. 2009).

Generally, most species found in other European lake districts are identical with those of the Bohemian Forest lakes. The family Dytiscidae is generally the most species-rich (especially genera *Agabus* and *Hydroporus*). *Agabus bipustulatus* (and *A. solieri* recently regarded as a cold-adapted form of the former variable species from higher altitudes; DROTZ et al. 2001) is probably the most common aquatic beetle in European mountain lakes. Since many of the aquatic beetles inhabiting lakes areas are widespread, the same species can be found in lakes in the Pyrenees, the Alps, the Carpathians, Fennoscandia, and the Bohemian Forest. Naturally, some cold stenothermic or high mountain species usually occurring in alpine lakes are missing in the Bohemian Forest lakes (e.g., *Hydroporus foveolatus*, *H. sabaudus*, *Stictotarsus griseostriatus*, *Helophorus nivalis*, *H. glacialis*; cf. KODADA 1990, BOGGERO & LENCIONI 2006, ČIAMPOROVÁ-ZAŤOVIČOVÁ & ČIAMPOR 2011). Similarly, some species with only small areas, i.e., missing in other regions, such as *Deronectes platynotus* and *Nebrioporus assimilis* were recorded from our lakes.

As far as we know, there are only a few genera not found in the studied lakes compared to other regions, such as *Stictotarsus* and *Platambus* of the Dytiscidae observed in lakes in the Alps and Denmark (BRODERSEN et al. 1998, BOGGERO & LENCIONI 2006, FJELLHEIM et al. 2009), *Colymbetes* and *Platambus* of the Dytiscidae, and *Crenitis* of the Hydrophilidae, and *Riolus* of the Elmidae found in the Tatra lakes (KODADA 1990, ČIAMPOROVÁ-ZAŤOVIČOVÁ & ČIAMPOR 2011), and *Oulimnius* and *Riolus* of the Elmidae found in lowland lakes in Denmark (BRODERSEN et al. 1998). Except the representatives of the genus *Riolus* that usually prefers warmer or mineral rich streams in the Czech Republic, all above mentioned taxa have been recorded in the Bohemian Forest so far (RŮŽIČKOVÁ & KOTRBOVÁ 2000, SYCHRA, unpubl. data) and thus their occurrence in the lakes is possible. On the other hand, our findings of the families Scirtidae (genus *Cyphon*), Chrysomelidae (genera *Donacia* and *Plateumaris*) and some genera of the family Hydrophilidae (*Cercyon*, *Enochrus*) are unique. These taxa have not been mentioned in any of those studies that we compare our data with. Moreover, there are at least 25–30 species found exclusively in the Bohemian Forest lakes contrary to about 25 species collected in addition in all remaining European lake districts.

The species diversity of aquatic beetles in the Bohemian Forest lakes is usually at least five times (but often 10 times) higher compared to other lake districts. This is probably due to lower elevation, geographic position, of the Bohemian Forest on the “crossroad” of several biogeographic regions, and obviously largely by the sampling effort targeted directly on aquatic beetles in this study. There are only very few comparable studies from European lakes with adequate survey of beetle fauna: e.g., NILSSON et al. (1994) from Swedish lakes, or KODADA (1990) and ČIAMPOROVÁ-ZAŤOVIČOVÁ & ČIAMPOR (2011) from the Tatra lakes, whereas comprehensive information from, e.g., the Alps or Balkan mountain lakes are unfortunately missing. The beetle taxocenoses of the Tatra lakes are the most similar to those of the Bohemian Forest lakes. Aquatic beetles of the Fennoscandian lakes are different from lakes in mountain regions of central Europe due to occurrence of many common lowland and some boreal species (NILSSON et al. 1994).

According to literature data (ROUBAL 1930, 1939a,b, ŘIHA 1957, KODADA 1990, KOWNACKI et al. 2000, KODADA et al. 2003, HAMERLÍK et al. 2006, ČIAMPOROVÁ-ZAŤOVIČOVÁ et al. 2010, ČIAMPOROVÁ-ZAŤOVIČOVÁ & ČIAMPOR 2011), at least 54 species (21 genera, 6 families) have been collected in lakes and their inlets/outlets in the Tatra Mts., compared to 9 families, 29 genera, and 55 species in the Bohemian forest lakes (Table 14). However, a very comparable number of species was found on 95 alpine water bodies compared to our 8 lakes. This is due to harsh environmental conditions in higher altitudes. Six families (Halipilidae, Dytiscidae, Helophoridae, Hydrophilidae, Elmidae, Hydraenidae) and 17 genera (*Halipilus*, *Acilius*, *Agabus*, *Dytiscus*, *Hydroglyphus*, *Hydroporus*, *Hygrotus*, *Ilybius*, *Laccophilus*, *Nebrioporus*, *Rhantus*, *Helophorus*, *Anacaena*, *Hydrobius*, *Limnius*, *Elmis*, *Hydraena*) are living in the both lake districts. Of the 36 representatives of the most species-rich family Dytiscidae found in the Tatra lakes, only 18 species have not been collected in the Bohemian Forest lakes. On the contrary, 12 species, living in the Bohemian Forest lakes, are missing in the Tatra lakes. Marked difference between the lake beetle fauna of the Bohemian Forest and the Tatra Mts. is higher diversity of the family Helophoridae in the latter region. There is only a single common species, *Helophorus flavipes*, in both areas. While only one species (*H. granularis*) has been collected in the Bohemian Forest lakes, further eight species were collected in the Tatra lakes (*H. aquaticus*, *H. asperatus*, *H. brevipalpis*, *H. brevitarsis*, *H. grandis*, *H. griseus*, *H. montenegrinus*, *H. nivalis*). Contrary to the Bohemian Forest lakes, no species of the families Gyrinidae, Noteridae, Scirtidae, and Chrysomelidae have been so far recorded from the Tatra lakes.

## Chironomidae

At generic level, a similarity exists in the composition of chironomid fauna between the Bohemian Forest and north European lakes in the boreal zone. Of 42 genera encountered in Fennoscandian boreal lakes (MOUSAVI 2002), 22 genera were also found in our recent samples from the Bohemian Forest lakes up to now: *Ablabesmyia*, *Arctopelopia*, *Chironomus*, *Cricotopus*, *Cryptochironomus*, *Endochironomus*, *Glyptotendipes*, *Heterotrissocladius*, *Macropelopia*, *Microtendipes*, *Micropsectra*, *Pagastiella*, *Parakiefferiella*, *Paratanytarsus*, *Phaenopsectra*, *Polypedilum*, *Procladius*, *Prodiamesa*, *Psectrocladius*, *Sergentia*, *Tanytarsus*, *Thienemanniella*. However, the presence of other common lacustrine genera is very likely (e.g., *Cryptotendipes*, *Harnischia*, *Parachironomus*, *Paratendipes*, *Pseudochironomus*). Some of them (*Heterotanytarsus*, *Dicrotendipes*, *Stictochironomus*) has been found in the outlets of Čertovo and Prášilské lakes, and others (*Paracladius*, *Cladopelma*, *Omisus*, *Tribelos*, *Cladotanytarsus*) are known from the subfossil records.

In comparison with Fennoscandian boreal lakes, the genera *Protanypus*, *Monodiamesa*, and *Stempellina* probably do not occur in the Bohemian Forest lakes. A comparison the chironomid data from the Bohemian Forest lakes with chironomids from montane humic lakes in the Tatra Mts. would be most appropriate. Unfortunately, as recent limnological research has been focused on the Tatra lakes above the tree line, there are not enough data from those forest lakes.

## CONCLUSION

The Bohemian Forest lakes host rather distinct and somewhat eminent taxocenoses (both in their richness and species composition) compared to any other lake district. However, different groups of insects reveal different degrees of similarity. In many taxa, the most similar taxocenoses have been distinguished in the Tatra lakes, e.g., for Ephemeroptera and Trichoptera, or Coleoptera, when compared to the Bohemian Forest lakes. These lakes are certainly situated on the biogeographic crossroad (see above, Biogeographic composition). Thus, beside their overall similarity with the Tatra lakes, their Heteroptera taxocenoses show the highest similarity with those in the Alps and the generic composition of Chironomidae taxocenoses are similar to boreal lakes.

Yet, any comparison of the considered European lake districts could be biased by at least two causes. The first type of bias represents a sampling strategy – i.e., the chosen method(s), sampling effort, and frequency (see the above discussion). The second type of bias may come from (un)available information – i.e., the data access, literature search efficiency, abundant grey literature (including possible language barriers), knowledge of sites, personal contacts, etc. We are aware of this kind of a positive bias in the case of comparing the Tatra lakes to the Bohemian Forest ones. Even though the former are vastly situated above the forest line, the effects of common knowledge (cf. literature on Czechoslovak fauna), deeper insight into local literature, joint projects, or personal contacts may naturally increase our overall knowledge on biodiversity in the Tatra lakes.

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