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Recent and subfossil chironomids as a tool for tracing of environmental changes in mountain lakes of glacial origin

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Ph.D. Thesis

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I declare that for publications submitted as a part of this Ph.D. thesis, Jolana Tátosová was an important member of the team, and significantly participated in data collection, biological analyses and in preparation of manuscripts.

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I declare that neither this thesis, nor any of the publications attached within, have been submitted for the purpose of obtaining the title of Ph.D. or any other title at another institution.

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Introduction, summary and conclusions

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Introduction

High altitude lakes represent very unique and vulnerable aquatic ecosystems characterized mainly by extreme temperature regime and oligotrophic conditions, which reflect the specific species composition of there-living assemblages. The majority lakes in the North Temperate Zone were formed by the retreating glaciers during the deglaciation at the end of Pleistocene Ice Age that terminate about 12 000 years ago. Some of them don't exist yet – they have been subsequently filled; however, many lakes are still present. During the very long time of their existence, the lakes have gone through many changes, which may be reconstructed by chemical and biological analyses of lake sediments. At the present time of very strong influence of human activity on the natural environment, these lakes present the least affected ecosystems due to their remoteness and negligible direct human impact. The knowledge of the lake historic development in the natural environment provides distinguishing the natural oscillations and human activity induced changes of lake ecosystems. The extremely high sensitivity of mountain lakes to global changes, such as atmospheric pollutions, acid deposition and climate variability, as well as their ability to reflect these impact very fast, make them excellent indicators of environmental changes (Whatne et al., 1997). The mountain ecosystem overall have become a subject of interest of the scientific community in the whole word.

Non-biting midges (Chironomidae) represent the most numerous and diverse group of benthic communities in the waters of mountain areas. They are very well adapted to low water and air temperatures as well as low food supplies, and also their life history well reflects inclement conditions of the mountain climate (Armitage et al., 1995). As the life of chironomids are controlled by many environmental parameters – temperature, food availability, concentrations of dissolved oxygen, pH, salinity (Sæther, 1979, Raddum & Sæther, 1981), heavy metals and other pollutants (Beeson et al., 1999, Mousavi et al.,

2003, Rippey et al., 2008), they can be very successfully used for tracking of environmental changes and effects of climatic variability on mountain lake ecosystems.

Chironomid ecology

Organisms living in alpine lake have to overcome harsh environmental conditions - low nutrient concentrations and food availability, short growing seasons, strong seasonal dynamics in temperature, light conditions, solar radiation or lake level fluctuations (Bretschko, 1974). The biotic communities in alpine lakes are, therefore, relative simple having a few but well adapted dominant species. That is also why the deepest part of mountain lakes is usually inhabited only by Oligochaetes and larvae of Chironomidae (Pinder, 1995), whereas chironomids form more abundant and specific richer group of this profundal community as well as the most numerous item of the littoral zoobenthic communities.

Chironomids are two-winged, non-biting insects (Chironomidea, Diptera). Immature stages – larvae – of the most of the chironomids live in the fresh waters and their larval development can take from several weeks to years. Imagoes leave the water environment and live as flying terrestrial insect. This family is noted for its taxonomic richness, with nearly 10.000 species distributed globally (Craston, 1995), representing more than 20% of all freshwater insects in rivers and lakes. Probably no other major family of aquatic macroinvertebrates occurs over as wide a geographical range as does the family Chironomidae. The great geographical distribution and global species richness of the Chironomidae can partially explain the great breadth of ecological conditions to which chironomids are adapted (Armitage et al., 1995). They colonize all freshwater systems, from large lakes to the smallest ponds, and often dominate the benthos. Aquatic larvae are associated with all types of inorganic and organic substrates: from silts, sands, boulders to vascular plants, leaves and woods.

The life cycle of chironomids pass through four stages. The females lay eggs on firm substrata (macrophytes, stones or leaf litter) close to the lake- or riverside immediately after copulation and soon die. The first instar larvae called larvulae have a dispersal role. They hatch within a few days and swim using figure-of-eight motion away from the site of hatching until they settle onto substratum and start to feed. After that, larvae develop in next three stages (instars), whereas each stage is ended by moulting of next

instar larva when the old skin and head capsule are left behind. Duration of stages, as well as larval growth and development at all are dependent primary on temperature and food supply. (Armitage et al., 1995). For example, development of *Chironomus* larvae in tundra ponds in Alaska lasts seven years (Butler, 1982). However, most temperate species are multivoltine, univolitne or bivoltine. Large species living in the cold profundal of deep lakes may take more then one year to develop, whereas small species living in warm and shallow waters may complete 3–4 generation in one year (Armitage et al., 1995). The harsh conditions in high mountain lakes cause the larval develop is slow and chironomids produce usually only one generation per year or more years (**manuscript 1**). When the fourth instar larvae reach maturity, they develop in the pupal stage that lasts few hours or days. Mature pupae rise to the water surface where the emergence of adults takes place. Timing of emergence is dependent on water temperature and light intensity (Kureck, 1980). Adults usually live just a few days, at most a few weeks (Pinder, 1986). As the many of high mountain lakes are naturally fishless, chironomids, especially the profundal community, are not exposed to strong predation, and their life is mainly controlled by abiotic factors and lake trophy. For these reasons, they have been used for lake typology, in particular for assessing lake trophic status and water quality ((Sæther, 1979).
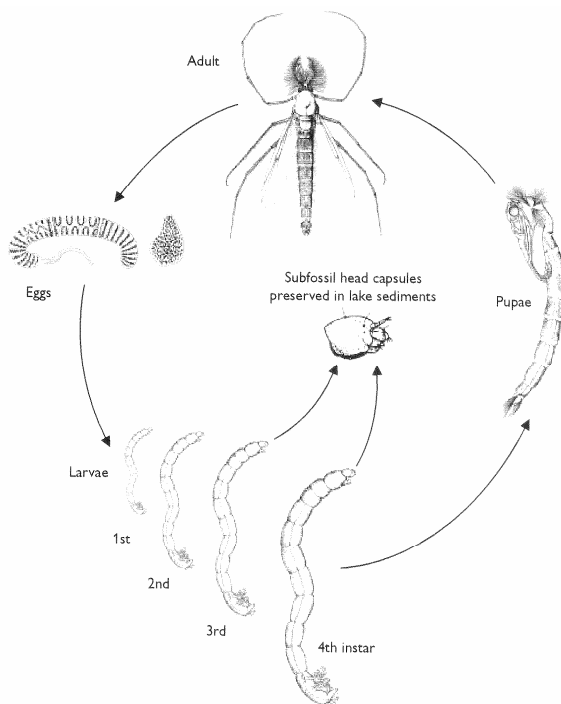
Fig. 1. Life cycle of chironomids (Brodersen & Anderson, 2000).

High mountain and subarctic lakes are known by their specific chironomid composition and low diversity at all. The general rule is that the number of chironomid taxa increase with decreasing altitude (Ashe et al., 1987). Orthocladiiane, Diamesinae and Chironominae of Tanitarsini tribe are usually the most frequent subfamilies observed in high altitude lakes. The factors, determining the chironomid species composition in the

profundal zone of the stratified lakes, are quality of food ant the oxygen conditions (Armitage et al., 1995).

As a result of their short generation times and the dispersal capacity of the winged adults, the chironomids appear to respond rapidly to environmental changes. In addition, the survival of chironomid larvae depends on number of different environmental parameters, including water temperature, habitat and food availability, and the chemical characteristics of the lake water, such as oxygen content, salinity or pH (Armitage et al, 1995) (**manuscript 2**). All these facts together with their dominant position among lake organisms make them one of the most important tools for a study of impacts of global changes on vulnerable mountain water ecosystems.

Chironomids as a tool in paleolimnology

The paleolimnology has undergo a major progress within last ten years, especially because of developments in statistics and methodology, the building up of high quality modern calibration data-sets, the improving of coring techniques, geochronology and subfossil remains identification. Paleolimnology provides the timing of past climate change, qualifies rates and magnitudes of these changes, and finally can determine the influence of human impact on freshwater ecosystems. During the last ten years, much attention has been focused on the use of various subfossil organisms preserved in lake sediments (Smoll et al., 2001, Walker, 2001). This is because lake ecosystems have been shown to be highly responsive to even minor changes in climatic and environmental conditions (Rouse et al., 1997), and also because aquatic organisms are the most reliable indicators of limnological and environmental conditions since they respond rapidly to changes in their habitats. Some of them (e.g. diatoms, chironomids, chrysophytes) are usually well

Fig. 2. Head capsule of subfossil chironomid species *Polypedilum A*-type (J. Tátosová).

preserved in lake sediments which makes them suitable for reconstructions of the past environment of lakes and their catchments. Most European lakes are of glacial origin hence the age of their sediments covers the period of the Late Pleistocene and Holocene.

One of the proxy indicators tracked in lake sediments are head capsules of chironomid larvae. Third and fourth instar chironomid larvae possess a chitinized head capsule that is resistant to decomposition. Consequently, fossilized chironomid head capsules tend to be well preserved in lake sediment over thousands of years, and can generally be identified to genus or, more rarely, to species-group level (Walker, 1987, Brooks et al., 2007). This offers the possibility of using the fossil chironomid record to infer past environmental conditions in lakes. Recent knowledge of chironomid ecology allows using fossil chironomid remains for the reconstruction of paleoproductivity (Brodersen & Lindegaard, 1999), nutrient loading (Brooks et al., 2001, Meriläinen et al., 2000), catchment and stream contribution (Heiri & Lotter, 2007), dissolved oxygen content (Brodersen et al., 2004, Quinlan et al., 1998, Quinlan & Smol 2002), acidification (Brodin & Gransberg, 1993), paleosalinity (Walker et al., 1995, Heinrichs et al., 2001), water depth (Korhola et al., 2000) and climate variations (Walker et al., 1991, Batterbee, 2000). Recently, the subfossil chironomid analysis is the important part of the climate paleoreconstructions (**manuscript 3**).

Reconstruction of paleotemperature

Paleotemperature reconstructions provide important information on the variations and dynamics of the climatic system and present temperature trend should be considered in relation to the natural long term climate variability. Temperature reconstructions help understanding of global climate dynamics and improving climatic models used for the prediction of future climate. Instrumental meteorological records are usually too short to cover the full variation in climate (last 100–150 years); the history of climate for earlier period has to be reconstructed from other, indirect "proxy" indicators (Korhola et al., 2002).

Studies in the 1990s showed that temperature is usually the most important environmental variable in explaining the broad-scale geographic distribution and abundance in chironomid taxa (Walker et al., 1991). A number of studies in northern temperate and sub-artic regions − using multivariate statistical techniques − have

demonstrated that mean summer air temperature and/or summer surface water temperature have a statistically significant relationship to the distribution of chironomids (Brooks & Birks, 2000). This quantification of chironomid response to temperature has enabled creating quantitative inference transfer functions (models) and the reconstruction of the Holocene temperature using subfossil chironomids deposited in the lake sediments. Models are based on surface-sediment samples from a large number of lakes covering the temperature gradient. To maximize the temperature gradient, the lakes chosen for the calibration set must span a broad range of climatic zones as represented by different altitudes and latitudes. It provides basic data from which quantitative estimates of the modern temperature optimum and tolerances of each taxon in the calibration data-set can be made. Regression and calibration techniques are used to develop a chironomid-temperature inference model from this modern calibration set. Mathematically, the models are developed using the WA-PLS method (weighted averaging partial least squares regression) with coefficient of determination (r^2) of 0.74-0.94 and RMSEP (root mean square error of prediction) of 0.88-1.54 °C. Recently, modern chironomid-temperature calibration data-sets have been developed for different European lake districts: Finland (Olander et al., 1999), Sweden (Larocque et al., 2001), Scotland (Brooks & Birks, 2000), Norway (Brooks & Birks, 2001) and high mountain lakes in the Alps (Lotter et al., 1997, Heiri et al., 2003). These models have bees successfully used for the reconstruction of millennial-scale climatic oscillations during the late glacial (Brooks, 2006) and patterns of temperature changes in many European areas (e.g. Andreev et al., 2004, Brooks & Birks, 2000, 2001, Dalton et al., 2005, Engels et al., 2008a, von Gunten et al., 2008, Hammarlund et al., 2004, Heinrichs et al., 2006, Heiri et al., 2003, 2007, Heiri & Lotter, 2005, Heiri & Millet, 2005, Korhola et al., 2002, Langdon et al., 2004, Larocque & Hall, 2004, Sarmaja-Korjonen et al., 2006, Rosén et al., 2003).

As Engels et al. (2008b) rightly suggested, even if many modern training sets have been designed for reconstructing mean July air temperatures, it does not mean that the chironomid fauna responds exclusively to air temperature (Birks, 1998). In fact, chironomids respond to both air and water temperature; water temperature influences the development of the relatively long larval stage, whereas air temperature has direct influence only on the survival and distribution of the winged, short-lived adult stage

(Brooks & Birks, 2001). Although Livingstone and Lotter (1998) have found that mean air and water temperatures are likely to correspond most closely in July, suggesting that calibration and reconstruction efforts should be concentrated on this month, there are still some potential interference mechanisms between July air temperature and water temperature; for instance, an increased impact of winter snow precipitation or glacier-fed streams on the temperature of the lake water (Birks & Birks, 2006, Brooks & Birks, 2001). In order to investigate whether these potential mechanisms played a role in the former lake or whether past changes in nutrient availability have influenced the chironomid-based temperature inferences, the application of a single proxy will not suffice. Multi-proxy studies providing multiple lines of evidence for possible changes in climate or environment will help to identify factors influencing the composition of fossil chironomid assemblages.

Research background of the mountain lakes in Czech Republic and Slovakia

In the Czech Republic and Slovak Republic there are only two regions where lakes of natural origin occur: (1) the Bohemia Forest with 8 small glacial lakes situated in the forested slopes of the mountains along the Czech-German-Austrian border and (2) the High Tatra Mts. on the Slovak–Poland border, where about 130 glacial lakes are situated at altitude from 1200 to 2145 m, most of them above timberline.

Investigation of benthic fauna in the Tatra lakes has a long tradition. The first information on benthic macroinvertebrate have been carried at the end of the 19th century by Vejdovský (1884) and Daday (1897), later by Minkiewicz (1914), Zavřel (1935a,b, 1937), Zavřel & Pagast (1935), Hrabě (1940, 1942), and Obr (1955). Bentic fauna have begun being intensively studied from the 1960s in connection with eutrophication (Juriš et al., 1965, Ertlová, 1964, 1987) and later with anthropogenic acidification (Krno et al., 1985, 1986, Krno, 1991a, b, Vranovský et al., 1994, Tátosová & Stuchlík, 2003). The research of Tatra lakes continuing to the present (Krno et al., 2006, Krno, 2006, Bitušík et al., 2006) is a result of young enthusiastic benthologists (Bulánková & Zaťovičová, 2006, Hamerlík et al., 2006, Kubovčík & Bitušík, 2006, Tátosová & Stuchlík, 2006 – **manuscript 1**)

The first hydrobiological research of all the Bohemian Forest lakes was performed almost 140 years ago by Frič (1872, 1893) and Frič & Vávra (1897). Although their

attention was focused mainly on planktonic life in the lakes, they have brought also some notes concerning water insect inhabiting littoral part of lakes as well as invertebrates in the soft sediment in the profundal. Since then occasional hydrobiological research has continued. After the World War II, the Bohemian Forest lakes have become inaccessible for scientists, as the lakes was located mostly behind actual wire fences in a broad military zone until 1990. That is why there are some unpublished data from 1940s, 1950s and 1970s, which were later mentioned by Soldán et al. (1999) and Vrba et al. (2003) and from 1960s later published by Procházková & Blažka (1999). As well as in the High Tatra Mts., some benthological studies in the Bohemian Forest are connected with acidification processes (Horecký et al., 2006, Soldán et al., 1996, 1998, Vrba et al, 2003) or other environmental gradients (Bitušík & Svitok, 2006, Papáček & Soldán, 1995).

In the 1970s, the surface waters in the whole world including the lakes in the Czech Republic and Slovakia were more or less affected by acidification. The decrease of lake water pH was a result of the long-distance air transport and deposition of sulphur and nitrogen compounds on catchments with geologically sensitive bedrocks (Fott et al., 1987, 1994) and/or poorly developed soils (Whright, 1983). Since the time, the intensive systematic limnological research proceeded in both mountains area focusing especially on the effect of the acid deposition on the chemistry and biota of lakes (Dargocká et al., 1997, Fott et al., 1992, 1994, 1999, Hejzlar et al., 1998, Kneslová et al., 1997, Kopáček & Stuchlík, 1994, Kopáček et al., 2004, 2006, Pražáková & Fott, 1994, Sacherová et al., 2006, Straškrabová et al., 1999, Stuchlík et al., 2002, Veselý, 1994, Veselý & Majer, 1996, Veselý et al., 1993, 1998, Vranovský, 1991, Vrba et al., 1993, Vranovský et al., 1994, Vyhnálek et al., 1994).

Over the last decade, high mountain and mountain lakes in Czech Republic and Slovak Republic are undergoing recovery from acidification as a result of the decreased emissions of sulfur and nitrogen compounds after political changes in East Europe in the 1990s (Kopáček et al., 1998, 2002). Nevertheless, in areas where the saturation of soils by nitrogen and sulphur took place during acidification, the process of recovery is slowed down by hysteresis (Kopáček et al., 2002, 2006). In addition, the re-occurrence of extinct species did not succeed immediately the increases of pH and alkalinity of lake

waters (Sacherová et al., 2006, Hořická et al., 2006, Stuchlík et al., 2002, 2006, Stuchlík, 2003, Nedbalová et al., 2006a, 2006b, Vrba et al., 2003) - **manuscript 2.**

Upon the previous studies at individual European mountain areas the project EMERGE has arisen. It was focused on the distribution of transboundary air pollution, distribution patterns of aquatic organisms and fish status, and lake ecological reference states for the European mountain lake population as a whole (>20 000 lakes). The research has propped upon empirical and process-based modeling of the main ecological features of the lakes, based on existing large datasets and specific site-based studies. For this specific-site study Ľadové pleso was chosen as the High Tatra Mts. key site, which allowed intensive one-year observation of annual cycle of lake water and precipitations chemistry and lake biota (Křeček et al., 2006, Nedbalová et al., 2006a, Šporka et al., 2006, **manuscript 1**).

A very current problem of climate changes has directed research scope in the High Tatra Mts. and the Bohemian Forest in recent years, so a next research attention was given to the long-term climate changes recorded in lake sediments. Namely in Tatra lakes, the patterns of seasonal variability and their implications for an interpretation of climate changes overt the last 200 years were investigated (Catalan et al., 2002, Stuchlík et al., 2002, Šporka et al., 2002). At the Bohemian Forest then, the Holocene and Late Pleistocene paleoenvironmetal reconstructions presently proceed, based on the multi-proxy analyses of the sediment from Plešné Lake. – **manuscript 3.**

Long-time limnological study of both mountain areas has allowed their including into the integrated studies on European lake ecosystems within multidisciplinary and international projects of the European Commission: AL:PE 2 - Acidification of mountain Lakes: Palaeolimnology and Ecology (1993–1995), MOLAR - Measuring and Modelling the Dynamic Response of Remote Mountain Lake Ecosystems to Environmental Change: A Programme of MOuntain LAke Research (1996–1999), EMERGE - European Mountain lake Ecosystems: Regionalization, diaGnostics and socio-economic Evaluation (2000–2003), EURO-LIMPACS - Integrated project to evaluate impacts of global change on European freshwater ecosystems (2004-2009) and RECOVER:2010 – Predicting recovery in acidified freshwaters by the year 2010 (1999-2002).

Scope of the PhD thesis

1. For the understanding how the chironomid community is able to reflect environmental changes in the high mountain areas, there is necessary to know their life cycle as best as possible. The study of seasonal dynamics of chironomids has never been done in Tatra Mts. lakes; therefore, it has become the first aim of my Ph.D. project.

2. According to the previous studies in the High Tatra Mts., acidification had a serious impact on lake water biota, namely on zooplankton and phytoplankton communities. Nevertheless, the one unanswered question remains: how does the profundal fauna (mean chironomids) reflect the long term acidification-recovery process?

3. The last part of my thesis is focused on the Holocene paleoenvironmetal reconstruction in the Bohemian Forest based on the chironomid stratigraphy in the lake sediment. I also attempted to quantitative reconstruction of the mean July air temperature for the Holocene period of ca. 10 thousand years.

Summary

Chironomid seasonality in a high mountain lake ecosystem – case study

This paper summarizes result of the first complete round-year study of chironomids in the profundal zone of an oligotrophic high mountain Tatra lake – Ľadové lake – chosen as the key site in the EMERGE project.

High mountain or arctic lakes are typical by the specific chironomid species composition, low species diversity at all and low abundances as well (Bretschko, 1974, Rieradevall & Prat, 1999, Aagaard, 1986, Brundin, 1956, Steinböck, 1955) Four chironomid taxa identified in the profundal of Ľadové lake (after average abundances) – *Micropsectra radialis* (Goetghebuer, 1939), *Pseudodiamesa nivosa* (Goetghebuer, 1928), *Procladius (Holotanypus)* sp. and *Heterotrisscladius marcidus* (Walker, 1856) – and the average chironomid density of 1 700 ind m^{-2} have confirmed this fact. The two most abundant taxa *P. nivosa* and *M. radialis* have demonstrated a univoltine life history with emergences in July and in August, respectively. According to published data, the univolitne life cycle of chironomids is expectable in high mountain or subarctic lakes (Moore, 1979, Wiederholm, 1977, Pechlaner et al., 1972, Laville & Gaini, 1974), even if in some arctic areas chironomids can need more than one year to complete development (Welch, 1976, Lindegaard, 1992). Anyway, the 5–6 month ice free period at Ľadové lake ensures long season enough for a chironomid growth.

We could see that the values of chlorophyll-*a* and TPV (total volume of particles) in vertical samples did not provide the right answer for the amount of food available for the profundal fauna. As the results from the sedimentation trap in 13 m depth have showed, the short-term December peak of chlorophyl-*a* and TPV recorded in the water column have been followed by a long period of very slow sedimentation, and it did not display as a peak of TPV accumulation rate in the deepest trap. As lately as allochtonous sources entering the lake during the ice melting and spring circulation have increase a food supply in the profundal at short time.

The annual variability in chironomid abundances close correlated with an amount of dissolved oxygen above the lake bottom. Even if Ľadové lake is the oligotrophic one, the high concentration of December phytoplankton common in mountain lakes (Fott et

al., 1999) could cause observed depletion of dissolved oxygen above the lake bottom during the oncoming period of winter stratification. That probably was the reason for the relocation of on oxygen sensitive larvae from the deepest sediment (the abundances of larvae was zero or very low) to the upper part of lake bottom (sublittoral) and migration to the upper layer of water column (as evidenced by the swimming larvae) during this period. Such migrational behaviour is one of many adaptations to low oxygen conditions, but never has been described in a mountain lake before. To confirm the migration hypothesis, a detailed study is necessary with the possibility of taking sublittoral samples, which part of this lake bottom is formed by large boulders.

Lake Acidification and chironomid responses

As the first synoptic researches showed, acidification caused a decline of lake water pH and alkalinity as well as an increase concentrations of anions of strong acids and aluminum (Schindler, 1988, Kopáček & Stuchlík, 1994), which have led to the changes in lake water trophy status and consequently to very important changes in the structure of lake water community (Stuchlík et al., 1985, 2002, Fott et al., 1992, 1994, 1999). According to the responses (changes) in both of lake water chemistry and phytoplankton/zooplankton during the peak of acidification from the mid 1980s to early 1990s, lakes above timberline were categorized into three groups: non-acidified lakes, acidified lakes, and strongly acidified lakes (Fott et al., 1994).

The original chironomids species composition in non-acidified lakes did not change during the period of acidification except for the disappearance of the predaceous littoral species *Zavrelimyia* sp. and the appearance of the acido-tolerant *Zalutschia tatrica*. This species occurred in the littoral of seepage lakes affected by the seasonal acidification of surface water layers during snowmelt. Within the period of recovery from acidification, this species disappeared. Chironomid fauna of acidified lakes was also remained unchanged even in the period of strong acidification and along the process of recovery, *C. scutellata* and *Paratanytarsus austriacus* have newly appeared in some lakes of this category, which could point to increasing food availability as these taxa are considered to be more food demanded. Deep stratified lakes have experienced acidification especially in the upper epilimnetic layer and thus the profundal fauna in the deepest part of these lakes remained ensured from a direct effect of low pH (Stuchlík, unpublished

data). Also decrease of phytoplankton concentration due to oligotrophication in acidified lake did not have such strong effect on chironomids as did on zooplankton. Input of allochtonous organic matter from catchment probably supported littoral species and profundal species may took advantage of biofilm on sediment-water interface. Nevertheless, the most evident changes have occurred in strongly acidified lake during the period of acidification. From the original chironomid fauna, the sensitive species vanished (*Micropsectra* sp., *T. lugens* and *Zavrelimyia* sp.) and new acid-tolerant appeared (*Tanytarsus gregarius*, *Zalutchia tatrica*, *Chironomus* sp.) persisting to this day. This group of lakes is represented by small and relatively shallow lakes (1.6-4.2 m) and acidified water probably reached to the lake bottom, which directly affected the profundal biota. *Chironomus* sp., species well know from productive dystrophic forest lakes in the High Tatra Mts. indicates an increased concentration of food during acidification. This may support hypotheses about acidification induced eutrophication of strongly acidified lakes.

Reconstruction of past environmental conditions based on subfossil chironomid stratigraphy in lake sediments.

The Bohemian forest lake sediments were previously studied by Veselý et al. (1993) and Veselý (1998, 2000) for pollen and metal pollution to evaluate the development of human impact in this remote mountain area over period of last four millennium. Except of contamination by Pb and Cd about 2 000 ago, they also found abrupt changes in the pollen stratigraphy around 3 100 BC and 800 BC which credited with climate shifts. To assess whole lake history, a 543 cm long core covering period of ca. 14.5 cal ka BP was collected from the Plešné Lake. Chironomid remains was analyzes in the upper 280 cm representing 10.4 cal ka BP.

The recent chironomid fauna is formed mainly by Orthocladiinae, and this group also dominated across the whole Holocene sediment. It points out that the trophic status of the lake could have been oligotrophic to mesotrophic, but probably never became eutrophic in its history. At the beginning of the Holocene (ca. 10.4–10.1 cal ka BP), only oligotrophic and cold-adapted taxa *(Diamesa* sp., *Micropsectra insignilobus*-type and *Heterotrissocladius grimsha*wi-type) have occurred clearly reflecting a cold climate oscillation during the Preboreal period. The high rate of sedimentation recorded at this

period resulted from a material input from the lake cathment having open tundra vegetation. Following variations in the chironomid fauna after the Preboreal period were reflected mainly by changes in abundances of dominant taxa rather than by changes in species composition. The history of littoral chironomid fauna was closely connected with macrophyte fluctuations (namely quillword *Isoëtes*), i.e. lake level fluctuations, resulting from changes of precipitation during the Holocene. At the end of Epiatlantic epoch (6–4.5 cal ka BP), the Plešné lake have probably passed dry climate as abundances of most dominant littoral taxa decreased as well as *Isoëtes* pollen and semi-terrestrial species (*Lymnophyes/Paralymnophyes*) became more abundant. Chironomids overall experienced the raise of Chironomini portion during the Middle Holocene, which was partly a result of generally very warm climate and partly of increased afforestation leading to the higher input of organic matter into the lake. The profundal community has not changed dramatically since Boreal for almost 7 000 years, although an evident decrease in the abundance of dominant *Heterotrissocladius marcidus* was recorded already from ca. 6 cal ka BP. The significant decrease and following extinction of this profundal taxa around ca. 2 ka cal BP, referred to changes in profundal conditions, most likely the increasing of organic matter in the sediment and possible oxygen depletion. The presence of *Plantago lanceolata* and *Rumex acetossela* pollen indicating grazing, points to the development of cultural fields and settlements at this time, which could have leaded to the increasing of the lake trophic status (Jankovská, 2006). These mesotrophic conditions persisted to the present, as the presence of *Chironomus anthracinus*-type in the upper layers confirm. The gradual progression of the chironomid fauna was interrupted by an event in the 1540–1771 interval, when most taxa have entirely vanished. Although, the dating of this event falls into LAI period, the problem of very low sums recorded in this sediment layers makes the fossil record less reliable.

Chironomid-inferred Holocene summer temperatures

A number of regional chironomid-inferred temperature models have been development and successfully used for reconstruction of the Lateglacial climate fluctuations (Walker et al., 1991, Lotter et al., 1997, Olander et. al., 1999, Brooks & Birks, 2000, 2001, Larocque et al., 2001, Heiri & Lotter, 2005, Heiri et al., 2007). However, the Holocene

time period records relatively small temperature variability that is often within the prediction errors of the temperature inference models (Broecker, 2001), compared with more pronounced changes occurred during the Lateglacial. Nevertheless, the Holocene temperature reconstruction from Alps (Heiri et al., 2003) demonstrate the ability of chironomid-based temperature inference models to record not only the high magnitude of temperature variations in the Lateglacial, but also a smaller climate signals in the Holocene.

In co-operation with dr. Heiri from the Utrecht University in Netherland, we used the chironomid-July air temperature inference model developed for the Swiss Alps. This transfer function has been calculated by weighted average-partial least squares regression (WA-PLS) (ter Braak, 1995) from a calibration data set relating chironomid distribution from 89 Swiss lakes (Lotter et al., 1997). WA-PLS with two components yielded a chironomid-July air temperature inference model with an r^2 of 0.81 and a root mean square error of prediction (RMSEP) of 1.51°C. For more statistical procedure see Heiri et al. (2003). This numerical model was successfully used for the Holocene paleotemperature reconstruction based on subfossil chironomids from three Swiss Alps, as well as for the Lateglacial temperature estimation from Netherlandish lowland lake. It confirms a fact that the chironomid-temperature models can be applied outside of the geographical area they have been developed for.

The inferred July air temperature varied from 10.6 to 14.0°C. The oldest samples coinciding with the period of Preborel (10.3–9 ka cal BP), produced a temperature range 10.6–12,.2°C and showed decreasing trend. During the Boreal interval (9–8 ka cal BP), the largest warming would supposes to take place persisting over next 2 000 years. The temperature inferred for this interval varied between 11.4–12.4°C with a decreasing tendency reversing around 8 ka cal BP. The reconstructed temperature for the followed period of the Late Holocene shows an opposite trend than that is known for European climate history, and exhibits large fluctuations (Fig. 3). Overall, reconstructed temperature demonstrates increasing trend during the Late Holocene with a reverse in period of 3-2 cal ka BP.
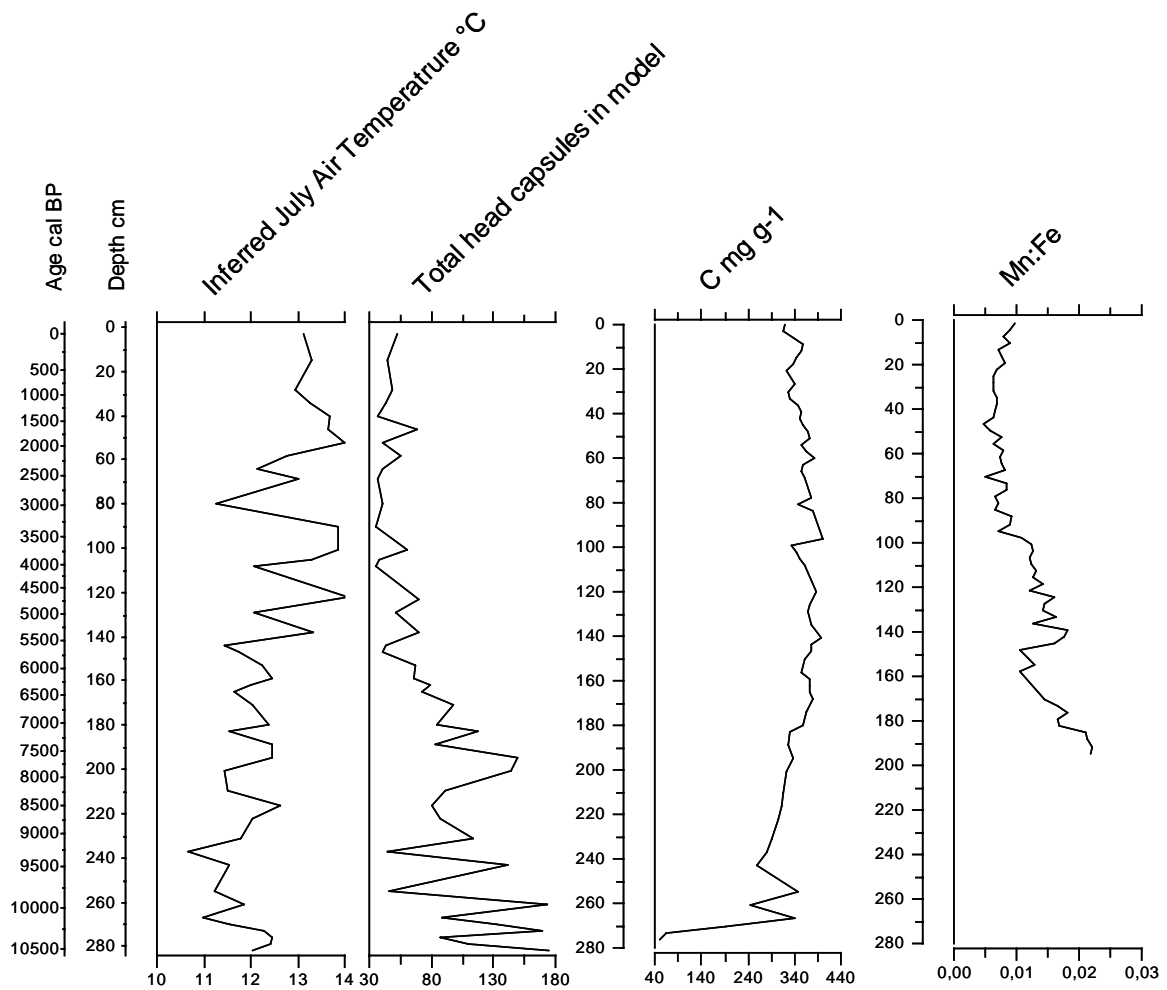
Fig.3. Chironomid-July air inferred temperature, organic Carbon (C) and Mn:Fe-molar ration in the sediment of the Plešné lake.

The quantitative temperature reconstruction from Plešné lake does not follow the common trend of the maximum temperature recorded in the early Holocene and subsequent cooling, as was documented by chironomid record from other sites throughout much of the northern hemisphere (for reviews see Larocque & Hall., 2004). Although, climate was probably the most important factor affecting not only chironomid fauna in lakes of Europe and North America, during the Holocene, local changes in the hydrology, vegetation history and soil development in the lake catchment could mask the impact of temperature on water biota, including chironomids. Other factors, such as water level fluctuation, nutrient laoding, and changes in dissolved oxygen concentrations may have also overridden the effects of temperature on midges during

certain periods of the Holcoene (Heinrichs et al., 2005, 2006, Antonsson et al., 2006). These factors are either directly or indirectly related to climate as well.

As was recorded in the chironomid stratigraphy, the abundance of the most dominant taxa has apparently reduced already from ca. 6 cal ka BP and later, the significant decrease (around ca. 2 ka cal BP) and following extinction has occurred (since 1.5 ka cal BP). One of the possible explanations is a depletion of dissolved oxygen content resulting from the increased organic material input from the lake watershed, which made unfavorable conditions for this chironomid taxon. Over the period ca. 6–5 cal ka BP, the greatest afforesttion took place in the catchment of Plešné lake, when *Abies*, *Picea* and *Fagus* have formed climax forest that has become a source of organic matter for the lake. Since ca. 2 cal ka BP, the pollen analysis showed a first distinct human impact on the original vegetation: the mixed oak wood retreated and synantropic herb vegetation began its most intensive expansion. Human activities near the lake have resulted in an increasing of nutrient loading that probably has led to the oxygen deficiency or anoxia (Fig. 3). Also Heiri & Lotter (2003) found in the Swiss Alp lake Sägistalsee that the early human presence in the lake cathcment and the lake susceptibility to the anoxia can lead to the incorrect Holocene temperature reconstruction.

The geochemical analysis of Mn/Fe ratio in the lake sediments is commonly used as indicator for paleo-redox conditions (Davison, 1993). In oxygenate waters, Fe and Mn form insoluble precipitates and are transported to deeper areas. Generally, the reduced form of Fe is less stable in the water column than that of Mn and consequently Mn/Fe ratios in the sediment are low when the sediment becomes anoxic (Koining et al., 2003). Decreasing trends of Mn/Fe molar ration in the sediment from Plešné lake (Fig. 3) suggest the oxygen depletion could be the explanatory factor that has overridden the effects of temperature on chironomid community.

Conclusions

A detailed seasonal investigation of the high mountain oligotrophic non-acidified lake could help us to better understand what kind of roles various parameters can play in the life history of chironomid in such water ecosystem. The species composition as well as total abundance of chironomid very well reflects the harsh conditions of extreme located lakes. In the period of ice cover, the profundal fauna is entirely depends on autochtonous food sources, which are heavily limited due to the very thick ice layer. Their life cycle is modified in that way to new generation would start its development during the period of food sufficiency and finish it before coming winter as a 4th instar larvae capable of over-wintering. The chironomid species living in high altitude lakes must be adapted to low annual temperatures, so they are represented by cold stenotermic and to oxygen sensitive taxa. As we found, these taxa are able to survive a short period of low oxygen concentrations by means of a migration up to the shallower locations, where the oxygen saturations is more positive.

Generally, reaction of profundal chironomid fauna to acidification in the High Tatra Mts. was delayed and less distinct compared to zooplankton. Chironomid community has responded to acidification in different ways depending on the stage of lake acidification that was depended on lake pre-acidification levels of base cations and buffering capacity. It seems that deep basins of previously acidified lakes have provided chironomids a shelter from a direct impact of low pH and the species composition of these profundal organisms has remained unchanged even in the period of strong acidification. On the other hand, shallow strongly acidified lakes have experienced serious shift in the chironomid composition to the acid tolerant species, which persists to this day. In addition, the presence of *Chironomus* sp. supports hypothesis on acidification induced eutrophication in this category of lakes.

The Plešné lake stratigraphy produced information on the long-term dynamics of the chironomid fauna shows the strong response of chironomids community to the cold conditions at the beginning of the Holocene. Further, the significant shift in abundance of dominant profundal taxa beginning at the Iron Age refers to evident human activities in the lake catchment area. As we found early, even high mountain lake can experience seasonal oxygen deficiency during the winter period, therefore this can be a possible

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explanation for the shift in profundal chironomids. The pollen stratigraphy suggests intensive grazing near Plešné lake at this time, since the increase nutrient loading has caused change of the lake trophy.

Results from Plešné lake indicate that the chironomid-inferred temperature reconstruction of the Holocene based on a sediment record from a single lake can get incorrect conclusions about past climate. A complex of interactions among various factors affecting the chironomids during the Holocene might alter the temperature signal (Brooks, 2006). In that case, the comparison the inferred temperature to other, qualitative temperature reconstruction from the same region is recommended. For example, combination of the paleobotanical analysis and chironomid-based temperature inferences provide considerable improvement of reliability of the paleotemperature reconstruction (Heiri & Lotter, 2005), as well as multiple temperature reconstruction (Larocque & Hall, 2004).

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