

Postglacial succession of caddisfly (Trichoptera) assemblages in a central European montane lake

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Running title:

Postglacial caddisfly succession in a montane lake

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Abstract:

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3 The Bohemian Forest lakes, situated along the Czech-German-Austrian border, were strongly
4 affected by atmospheric acidification between the 1950s and the late 1980s. The subsequent
5 chemical recovery of the lake water should precede and enable a biological recovery,
6 including changes in caddisfly (Insecta: Trichoptera) assemblages. Nevertheless, local pre-
7 acidification data and detailed knowledge of the lake district history are missing, making
8 evaluation of lake recovery difficult. We performed high-resolution analysis of caddisfly
9 remains in a 2.2 m long sediment profile from Prášílské Lake covering the complete history of
10 the lake-catchment evolution. Caddisfly larvae are good indicators of environmental
11 conditions and their subfossil remains are well preserved in unconsolidated waterlaid
12 sediments. A total of 10 caddisfly morpho-taxa were found providing a record from 11,400
13 cal. yr. BP to the present. With the exception of *Athripsodes aterrimus*, all identified species
14 are currently present in the Bohemian Forest glacial lakes or their inflow streams but not all of
15 them are documented in Prášílské Lake. The caddisfly fauna consisted of acid-resistant, acid-
16 tolerant and eurytopic species since the Early Holocene. Based on our results, the acid,
17 dystrophic state of Prášílské Lake has been occurring since the lake formation. We conclude
18 that the first signs of natural acidification appeared not later than during the Holocene onset in
19 the Bohemian Forest region. Furthermore, we did not detect any abrupt changes in the species
20 composition connected to the period of anthropogenic acidification during the 20th century.
21 This study provides for the first time a record of postglacial succession of caddisfly
22 assemblages in a central European mountain lake.
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31 **Key words:** natural acidification; Holocene; palaeolimnology; macrozoobenthos; lake
32 sediment; erosion events; Bohemian Forest
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Introduction

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3 During the last decades, many freshwater bodies across the Northern Hemisphere have
4 experienced anthropogenic acidification (e.g. Mylona 1996; Clair et al. 2007; Jia and Gao
5 2017). This process, caused by high inputs of acidic or acidifying compounds to the
6 atmosphere and their subsequent transport, also resulted in chemical changes in groundwater
7 and soil (Norton et al. 2013), as well as substantial changes in terrestrial and aquatic
8 ecosystems, including reduction of biodiversity and local species extinctions (e.g. Beamish
9 1976; Fott et al. 1994; Bobbink et al. 1998). In geologically sensitive regions, the negative
10 effect of decreased pH is usually associated with acidification-induced oligotrophication, low
11 phosphorus availability, lack of food resources for secondary producers, and ionic aluminium
12 toxicity (Vrba et al. 2015; Stuchlík et al. 2017). However, levels of acidification stress and
13 acidification recovery rate are always site-specific, depending on the ability of an ecosystem
14 to neutralize the flux of acidity (Stuchlík et al. 2017). In addition to the acidification caused
15 by atmospheric pollution, the process of natural acidification and phosphorus depletion plays
16 a crucial role on longer time scales (Kuneš et al. 2011; Boyle et al. 2013). pH history
17 reconstructions from many Northern Hemisphere lakes show more alkaline conditions after
18 the last local deglaciation (e.g. Engstrom et al. 2000). In the low- and mid-altitude temperate
19 regions with bedrock formed from metamorphic and crystalline rocks, the first signs of
20 acidification begun to manifest since the Early Holocene (Birks et al. 2000; Norton et al.
21 2011). According to the mineral-depletion hypothesis (Salisbury 1922; Boyle 2007), this shift
22 can be explained by leaching of the calcium phosphate mineral apatite from granitic till soils
23 or windblown material (loess) during the postglacial period(s). For alternative acidifying
24 mechanisms, such as direct climate impacts and successional vegetation cover changes, only a
25 lesser importance is assumed (Boyle et al. 2013).

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36 Among organisms sensitive to acidification in water environment, several groups have an
37 advantage of good preservation in waterlogged anoxic environments, allowing tracking of
38 acidification history using fossil assemblages. Especially diatom (Bacillariophyta) and
39 cladoceran remains (Crustacea: Branchiopoda) are widely used for pH reconstructions and
40 gained importance in the field of palaeoecology (e.g. Smol et al. 2008). Also, insect remains
41 are often abundant and well-preserved in Quaternary lacustrine and fluvial sediments, but
42 their bioindication potential has been little used in acidification-focused studies (Elias 2010).
43 Especially caddisflies (Insecta: Trichoptera) can provide a potentially important proxy, as
44 their recent ecology and pH preferences are, compared to the other water invertebrates,
45 relatively well known (Williams 1988; Fjellheim and Raddum 1990; Braukmann and Biss
46 2004; Graf et al. 2008; Schartau et al. 2008). Besides studies related to recovery from
47 anthropogenic acidification (e.g. Larsen et al. 1996; Langheinrich et al. 2002; Ross et al.
48 2008), current caddisfly assemblages are also used for bioindication of water quality and
49 hydromorphological degradation (Hering et al. 2004; Savić et al. 2013), bottom substrate
50 (Beisel et al. 1998), macrophyte presence (Buczyńska et al. 2017), and recovery from
51 environmental stress (Bradt et al. 1999). Williams (1988) acknowledged their value in
52 palaeoecological studies, as subfossil Trichoptera are abundant in limnic and fluvial
53 sediments. Subfossil caddis larvae remains consist especially of chitinous head sclerites,
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1 thoracic sclerites, and disarticulated leg segments (Williams 1988; Elias 2010). Caddisfly
2 cases or retreats can be also preserved in the sediments but usually in low numbers (Williams
3 1988). For identification, froclypeal apotome (frotoclypeus), one of the head sclerites, is the
4 most valuable. Caddisfly frontoclypeal apotomes differ based on shapes and textures,
5 including differences in colour pattern, muscle scar pattern and setal distribution (Elias 2010;
6 Waringer and Graf 2011). Although the presence of caddisfly larvae remains was occasionally
7 reported from Quaternary sediments (e.g. Elias and Wilkinson 1983; Solem et al. 1997), few
8 comprehensive palaeoecological studies using caddisflies have been conducted in Europe.
9 The first quantitative study based on well-dated record was published by Solem and Birks
10 (2000) showing climate-related Late Glacial and Early Holocene caddisfly succession in Lake
11 Kråkenes, Norway. Later, one Danish and several English studies on riverine deposits resulted
12 in detailed reconstructions of the flow environment of former river channels and the adoption
13 of subfossil caddisfly larvae remains in paleo-flow reconstructions (Wiberg-Larsen et al.
14 2001; Greenwood et al. 2003, 2006; Ponel et al. 2007; Howard et al. 2009). These studies
15 demonstrate that subfossil Trichoptera larvae are still an underused valuable palaeoecological
16 tool and can be applied in studies in other regions as well. Moreover, no study has yet utilized
17 caddisfly remains to reconstruct the history of natural or anthropogenic acidity.

25 Among lake districts affected by strong anthropogenic acidification, the Bohemian Forest, a
26 Czech Republic-Germany-Austria border area with geologically sensitive bedrock (mica-
27 schist, gneiss, granite), has been intensively studied during the last decades (Vrba et al. 2015
28 and references therein). Three glacial lakes on the German side (Großer Arbersee, Kleiner
29 Arbersee, Rachelsee) and five lakes on the Czech side (Černé Lake, Čertovo Lake, Laka
30 Lake, Plešné Lake, Prášílské Lake) are distributed over the Bohemian Forest (Figure 1) and
31 protected within the Šumava National Park, the Šumava Landscape Protected Area, and the
32 Bayerischer Wald National Park. Their atmospheric acidification started presumably in the
33 1950s and peaked in the late 1970s and first half of the 1980s, when surface water pH
34 decreased below 5 (Fott et al. 1994). Moreover, the total aluminium concentrations at the
35 most affected localities were $\sim 1 \text{ mg.l}^{-1}$ and elevated terrestrial export of toxic ionic aluminium
36 and lake water oligotrophication resulted in drastic changes in biota (e.g. Fott et al. 1994;
37 Vrba et al. 2000; Soldán et al. 2012). Despite a decline in sulphur and nitrogen deposition and
38 rapid improvement in water chemistry of all lakes in the last 30 years, biological recovery has
39 been relatively slow (Vrba et al. 2016). There is also a long, albeit fragmented, history of
40 macrozoobenthos research in the Bohemian Forest lakes (Soldán et al. 2012) and the first
41 mention of caddisfly larvae from Černé Lake can be found in Frič (1872). The recovering
42 lakes are a subject of regular monitoring since 1984, including aquatic insect larvae sampling
43 (e.g. Ungermanová et al. 2014; Vrba et al. 2016). Currently, a total of 46 species of
44 Trichoptera is known from these lakes and their inflow streams and outlets (Soldán et al.
45 2012). Although the signs of biological recovery (re-appearance of indigenous species,
46 decline in eurytopic and acid-tolerant species, or colonisation of vagile species) are obvious in
47 the lake biota, including macrozoobenthos (Vrba et al. 2016), the long-term history of the
48 lakes and their pre-acidification states are almost unknown. Thus, these gaps in knowledge
49 make it difficult to interpret the currently observed changes in invertebrate assemblages. In
50 this study, we reconstruct a postglacial caddisfly succession in one of the Bohemian Forest
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lakes – Prášílské Lake – using their subfossil remains. Here we aim: (i) to demonstrate the pre-acidification/preindustrial caddisfly species composition and its comparison with the species composition of the currently recovering lake; and (ii) to assess potential signs of natural acidification during the lake evolution.

Material and methods

Study site

Prášílské Lake (49.075° N, 13.400° E) is a moraine-dammed glacial lake in the Bohemian Forest (Šumava NP), Czech Republic, and is situated at an altitude of 1079 m a.s.l. (Fig. 1). The total surface area is 4.2 ha and the basin comprises a steep littoral zone that deepens rapidly to a maximum depth of 17 m. At the nearest meteorological station Churáňov (49.068°N, 13.615°E, 1122 m a.s.l.), the mean annual rainfall is 1090 mm, the mean January temperature -4.1°C, the mean July temperature 12.9°C, and the number of frost days is 165 (during the climatic period 1961 – 1990). Currently, three mountain streams drain a lake catchment of 65 ha that is dominated by Norway spruce (*Picea abies*) forest (Šobr and Janský 2016). According to published literature (Vrba et al. 2000; Soldán et al. 2012 and references therein), Prášílské Lake used to be a humic brown-water lake with more or less neutral pH before the onset of anthropogenic acidification. Heavy atmospheric pollution, resulting in acidification of the lake, occurred between 1950 and 1980 and the current pH is approximately 5.0 – 5.3 pH (Vrba et al. 2000; Soldán et al. 2012). The low water pH levels in this lake may explain the poor composition of the littoral vegetation, which consists of *Carex rostrata* and two species of *Sphagnum* (Soldán et al. 2012). Compared to other Bohemian Forest lakes, Prášílské Lake contains only moderate concentrations of dissolved aluminium (Kopáček et al. 1999). This may be the reason why two sensitive crustacean species (*Daphnia longispina* and *Cyclops abyssorum*) have survived in this lake to present, while they became extinct in all other sites (with exception of Großer Arbersee) during the peak of anthropogenic acidification and accompanied rise of ionic forms of aluminium (Kohout and Fott 2006; Kopáček et al. 2009). There is no documented evidence of any fish population in the lake since at least the mid-19th century when the lake was first studied, and it has been speculated that the site is too difficult to reach by fish (Vrba et al. 2000). Prášílské Lake has been subject of long-term ecological studies on the recovery of acidified Bohemian Forest lakes (e.g. Fott et al. 1994; Ungermanová et al. 2014; Vrba et al. 2016).

Sediment record and age-depth modelling

In August 2015, a 2.19 m sediment profile (1480 – 1699 cm below lake water surface) was collected in three 1.5 m long overlapping cores (PRA15-1-2, PRA15-2-1 and PRA15-2-2) using a Russian peat corer of 0.075 x 1.5 m chamber, using a floating platform in the central part of the lake basin (49.0752925° N, 13.4000039° E). A gravity corer (Boyle 1995) was used to recover unconsolidated deposits including the sediment-water interface. The retrieved gravity core (PRA15-GC-2) was 0.43 m long and 0.1 m in diameter. For sedimentological interpretation and correlation of the cores, the whole profile including its overlapping parts

1 was scanned with micro X-Ray Fluorescence (Olympus Delta Professional μ XRF) and line-
2 scan photographed at high-resolution (15 μ m) under uniform lighting using the University of
3 Liverpool Geotek Multi-Sensor Core Logger (MSCL). For obtaining chronological control,
4 the cores were dated using Accelerator Mass Spectrometry (AMS) 14 C dating, 210 Pb and 137 Cs
5 radioisotope dating, and a Bayesian age-depth modelling routine 'BACON' (see Carter et al.
6 2018a for additional details). The ages are reported in calibrated years before present (cal. yr.
7 BP; calibration sensu Reimer et al. 2013), where 'present' refers to 1950 AD. In this study,
8 we also present the rubidium (Rb) concentrations measured by μ XRF, which is interpreted as
9 a proxy record for detrital sediment supply recording changes in erosion and transport of
10 allochthonous inorganic matter from the catchment to the lake.
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15 *Sediment subsampling and caddisfly analysis*

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18 The long cores from Prášilské Lake were used for a multi-proxy study (see Carter et al.
19 2018a, b) and sub-sampled in 0.5 cm resolution, while core PRA15-GC-2 was subsampled in
20 1 cm resolution. During the subsampling, several thin (2 – 0.1 cm) grey and dark brown units
21 containing various plant and animal macro-remains were identified. These erosional layers
22 were targeted and the adjacent samples above and below were selected for analysis of the
23 caddisfly remains. Finally, most of the samples from non-overlapping parts of the long cores
24 and the gravity core were analysed. A total of 318 sediment samples with wet volume of 1.5 –
25 5 mL for the long cores and 5 – 20 mL for the gravity core were processed. The samples were
26 sieved over 100 μ m mesh size to retain all macro-fossils. Caddisfly larvae remains were
27 picked using a stereoscopic microscope at 15x magnification, dehydrated in 90% ethanol, and
28 mounted in Euparal to prepare permanent slides. To avoid an overestimation of individuals,
29 we focused only on frontoclypeal apotomes. Frontoclypei were identified using a reference
30 collection of Trichoptera larvae from Bohemian Forest lakes and streams, and the
31 identification key by Waringer and Graf (2011). Conventional identification keys to caddisfly
32 larvae are only partially useful since they use combination of many characters located on
33 different parts of the body. Therefore, the direct comparison with recent identified larvae was
34 essential. Where identification to species level was not possible, morphotypes were
35 established for the frontoclypei. Ecological characteristics of the individual caddisfly species
36 based on Wallace et al. (1990), Braukmann and Biss (2004), Graf et al. (2008), Schartau et al.
37 (2008), and personal observations were used to derive ecological properties of the identified
38 taxa. According to the latest agreements on the subdivision of the Holocene epoch (Walker et
39 al. 2012) and sediment lithology, we divided our stratigraphic record into 4 zones - the Early
40 Holocene (11,400 – 8,300 cal. yr. BP), a multiple-erosion event (8,300 – 7,600 cal. yr. BP),
41 the Middle Holocene (7,600 – 4,200 cal. yr. BP) and the Late Holocene (4,200 cal. yr. BP –
42 present). The multiple-erosion event represents a site-specific transitional unit covering the
43 proposed Early–Middle Holocene Boundary at 8200 cal. yr. BP (Walker et al. 2012).
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56 **Results**

57 *Chronology and lithology*

1 The age-depth model (Table 1, Fig. 2) dates the oldest sediments of Prášílské Lake to 11,400
2 cal. yr. BP. The whole profile consists of a brown organic gyttja, except for the basal 0.09 m
3 of sandy sediment at the base of PRA15-2-2. In addition, the long cores were characterized by
4 the presence of thin grey and dark brown units contrasting strongly with the lighter brown
5 colour of the gyttja. Most of these units contained increased concentrations of inorganic
6 material and plant and insect macro-remains. Because of very low thickness (< 2 mm) of
7 some units, we used the Rb curve to track these event laminations interpreted as erosion
8 layers instead of their visual description (Fig. 2 and 3).
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12 Thin erosional units (bands) occurred in an irregular interval at depths of 16.46, 16.38, 16.05,
13 15.94, 15.87, 15.79, 15.73, 15.39, and 15.03 m. Only two of them, 15.87 and 15.72, had a
14 thickness over 0.01 m. Moreover, the largest band of bright brown/greyish erosional sediment
15 was found between 16.215 – 16.355 m. It contained abundant macro-remains, only the
16 uppermost 8 mm (16.215 – 16.223 cm) was clayey and poor in remnants (> 100 µm) of
17 subfossil organisms. Radiocarbon dates below and above this distinctive 0.14 m thick unit
18 show a relatively long deposition time from 8,300 to 7,600 cal. yr. BP. Besides increased
19 inorganic content in the erosional units, the Rb curve demonstrates gradually decreasing
20 values (from 60 to 10 ppm) during the transition from sandy to more organic sediment in the
21 basal part of the profile and a peak (50 ppm) in the uppermost part of PRA15-2-2 (Fig. 2
22 and 3).
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29 *Trichoptera record*

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31 Altogether, 58 individuals from 10 taxa were found in the profile (Fig. 3 and 4). An overview
32 of the species occurring in Prášílské Lake and its inflow streams during the last century
33 (1918/1919 – 2015) along with the taxa identified from the lake sediment samples is
34 summarized in Table 2. In some cases, trichopteran frontoclypei could not be identified to
35 species level and were named according to the taxa to which the remnants were likely to
36 belong. Therefore, we established 4 morphotypes. Two distinct taxa of the genus *Limnephilus*
37 were recognized – *L. rhombicus*-type (frontoclypeus pale with a dark brown longitudinal band
38 broadened anteriorly) and *L. coenosus*-type (frontoclypeus uniformly dark brown without a
39 pale area in the posterior angle). A phryganeid morphotype *Agrypnia* – *Phryganea* includes
40 *Agrypnia* spp. and *Phryganea* spp., and a psychomyiid morphotype *Lype* – *Tinodes* could be
41 represented by species with an almost concolorous frontoclypeus (e.g. *Lype phaeopa* and
42 *Tinodes waeneri*) (Fig. 4). In addition, we documented presence of 6 species from 5 families:
43 *Athripsodes aterrimus* (Leptoceridae), *Cyrnus trimaculatus* and *Holocentropus dubius*
44 (Polycentropodidae), *Molanna nigra* (Molannidae), *Oligotricha striata* (Phryganeidae), and
45 *Philopotamus ludificatus* (Philopotamidae).
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54 Ecological evaluation of the caddisfly assemblages is presented in Table 3. Individual taxa
55 include species widely distributed in lentic waters (*Agrypnia* – *Phryganea*, *Holocentropus*
56 *dubius*, *Limnephilus coenosus*-type, *Molanna nigra*, *Oligotricha striata*), as well as in both
57 lentic and lotic waters (*Athripsodes aterrimus*, *Cyrnus trimaculatus*, *Limnephilus rhombicus*-
58 type, and *Lype* – *Tinodes*). Only *Philopotamus ludificatus* is a characteristic inhabitant of
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1 streams. Among these taxa, almost all basic functional-feeding groups are represented,
2 although passive filter feeders, shredders, and predators are predominant. Most of the
3 documented taxa use a wide range of food items. Similarly, the substrate preferences are
4 diverse, ranging from species which preferably occur in fine mud or sand to species which
5 depend on stable substrates like stones and water macrophytes. On the other hand, a
6 categorization to pH sensitivity groups is more uniform showing presence of acid-resistant,
7 acid-tolerant, and pH indifferent caddisflies. The only exception is the single finding of pH
8 sensitive *Philopotamus ludificatus*, an inhabitant of non-acidified streams (the specimen
9 probably originates from any of the lake inflow streams).
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13 To evaluate changes in caddisfly species composition in time, 4 zones based on the
14 climatological subdivision of the Holocene and sediment lithology were established (Fig. 3).
15 The first zone (1699 – 1631 cm; 11,400 – 8,300 cal. yr. BP; Early Holocene) covers the
16 development of the lake shortly after its formation and initially contains remains of
17 *Limnephilus coenosus*-type after which *Holocentropus dubius*, *Limnephilus rhombicus*-type,
18 *Agrypnia – Phryganea*, *Cyrnus trimaculatus*, and *Oligotricha striata* occurred. The second
19 zone (1634.5 – 1621.5 cm; 8,300 – 7,600 cal. yr. BP; multiple erosion event) covers the large
20 erosion band accompanied by peaks in Rb concentration. This zone contains the highest
21 numbers and volumetric abundances of Trichoptera remains (up to 27 frontoclypei per 10
22 cm³). The assemblage consists of relatively abundant *Limnephilus rhombicus*-type and
23 *Holocentropus dubius*, and less abundant *Cyrnus trimaculatus*, *Limnephilus coenosus*-type,
24 and *Molanna nigra*. In the third zone (1621.5 – 1567 cm; 7,600 – 4,200 cal. yr. BP; Middle
25 Holocene), we found frontoclypeal apotomes of *Holocentropus dubius*, and single evidence of
26 *Athripsodes aterrimus*, *Agrypnia – Phryganea*, *Cyrnus trimaculatus*, *Limnephilus rhombicus*-
27 type, *Molanna nigra*, *Philopotamus ludificatus*, and *Lype – Tinodes*. The last zone (1567 –
28 1480 cm; 4,200 cal. yr. BP – present; Late Holocene) is characterized by a very low
29 volumetric abundance of caddisfly remains (0 – 5 frontoclypei per 10 cm³). Only two
30 specimens of *Holocentropus dubius* were documented between the depths 1621.5 cm and
31 1483.5 cm. The top part of this zone (1483.5 – 1480 cm; 1960 – 2015 AD) contains *Agrypnia*
32 – *Phryganea*, *Limnephilus coenosus*-type, and *Limnephilus rhombicus*-type. The most
33 abundant taxa in the whole profile were *Holocentropus dubius* (31%), *Limnephilus coenosus*-
34 type (24%), and *L. rhombicus*-type (24%). The remaining taxa were less represented (<7%)
35 (Fig. 3).
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47 Discussion

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49 The subfossil Trichoptera larvae assemblages from Prášílské Lake include most of the species
50 which were found in the lake during the irregular environmental monitoring since 1918/1919
51 (Soldán et al. 2012 and references therein; see Table 2). Only *Chaetopteryx villosa* and
52 *Plectrocnemia conspersa*, common species in streams, rivers and small upland lakes (Wallace
53 et al. 1990; Andersen and Tysse 2008), currently inhabiting all Bohemian Forest lakes and/or
54 their inflow streams (Soldán et al. 2012), were not found in our samples. We also have not
55 found any evidence of *Limnephilus centralis* and *Limnephilus lunatus*, two species recorded
56 in the first half of the 20th century (Šámal 1920; Novák 1996). Both morphotypes of the genus
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1 *Limnephilus* presented in this study, *L. coenosus*-type and *L. rhombicus*-type, may include
2 more species with the same frontoclypeal colour pattern because the identification of living
3 larvae to species level is based on a combination of different morphological characters
4 including characters on soft body parts (Waringer and Graf 2011). However, since the species
5 *L. rhombicus* and *L. coenosus* are much more common in the Bohemian Forest lakes (Soldán
6 et al. 2012), it is highly likely that the remains identified as *L. rhombicus*-type and *L.*
7 *coenosus*-type, respectively, correspond with these two species. Similarly, *Agrypnia varia* and
8 *Phryganea bipunctata* were not found with certainty, but we assume that these species are
9 included within the *Agrypnia – Phryganea* morphotype. Nevertheless, for these
10 identifications, it has to be taken into regard that they might concern species which are rare or
11 absent in the recent Bohemian Forest lakes. On the other hand, several taxa, which were not
12 reported from Prášílské Lake at present, were found in the sedimentary archive – *Athripsodes*
13 *aterrimus*, *Cyrnus trimaculatus*, *Lype – Tinodes* morphotype, and *Philopotamus ludificatus*.
14 In the latter case, however, it is worth mentioning that the species is known from the lake
15 inflow streams. It cannot be ruled out that in the past a small portion of the caddisfly remains
16 could be transported from these inflow streams to the lake and deposited in the sediments.
17 Nevertheless, the majority of frontoclypeal sclerites cannot have been transported far from the
18 larval habitat. We assume this because of low discharge of the recent inflows and very small
19 proportion of stream Diptera remains found in the same sediment samples (D. Vondrák,
20 unpublished data). The caddisfly stratigraphic record (Fig. 3) should not be interpreted to
21 represent complete species composition or precise concentration of individuals through time.
22 Due to the low number of remains/individuals in the lake sediment we are not able to assess
23 detailed changes in volumetric or relative abundances. Our results are of a qualitative nature.
24 Therefore, we focus on interpreting the ecological preferences of the individual indicator
25 species.

26 Ecological characteristics of individual species found in the sediment record are summarized
27 in Table 3. *Holocentropus dubius*, a polycentropodid species and the most dominant taxon in
28 our sediment samples, generally occurs in the littoral zone with macrovegetation (Graf et al.
29 2008) and is also known from dystrophic (peaty) mountain lakes (Chvojka 1992). Despite its
30 frequent occurrence in Prášílské Lake in the past, it has not been recorded there during the
31 recent monitoring (1918/1919 – 2015) until its first observation in 2007 (J. Petruželová, pers.
32 comm). In the Bohemian Forest lakes, stable populations of *H. dubius* are only known from
33 Laka Lake and Großer Arbersee (Soldán et al. 2012; Ungermanová et al. 2014), two sites with
34 well-developed littoral macrovegetation (Fig. 1). The other dominant taxa (<20%) in the
35 sedimentary record are the two morphotypes of genus *Limnephilus* – *L. coenosus*-type and *L.*
36 *rhombicus*-type. *L. rhombicus* is a eurytopic species known from a variety of standing and
37 slow-flowing waters including acidic peaty waters (Wallace et al. 1990). It is widely
38 distributed in the Bohemian Forest (K. Novák, unpublished data) and it was recorded from all
39 glacial lakes with the exception of Rachelsee (Soldán et al. 2012). *L. coenosus* is a common
40 species in pools on peat bogs (Waringer and Graf 2011) and in small, strongly acidified lakes
41 (Krno et al. 2006). It is also well established in the Bohemian Forest, above all in peat bogs
42 (Novák 1996). The phryganeid taxon *Agrypnia – Phryganea* could include not only *Agrypnia*
43 *varia* and *Phryganea bipunctata*, but also *A. obsoleta* (McLachlan, 1865) and *P. grandis*

1 Linnaeus, 1758 since all species are known from the glacial lakes in this area (Novák 1996,
2 Soldán et al. 2012). *A. varia* and *P. bipunctata* occupy the same ecological niche – littoral
3 zone with macrophytes. *Oligotricha striata* is a common species in pools, especially with
4 acidic peaty water (Wallace et al. 1991). This species is known from all present Bohemian
5 Forest lakes, except of Černé and Čertovo lakes (Fig. 1), and also from peatbog pools in the
6 region (Novák 1996; Soldán et al. 2012). The larvae of *Molanna nigra* prefer a psammopelal
7 habitat (sand or clay) of mid-montane and lowland lakes (Graf et al. 2008). *M. nigra* is a
8 species with boreo-montane distribution and is known from northern Europe (Graf et al.
9 2008) and also from Siberia (Ivanov 2011). In central Europe, it has isolated populations in
10 the Bohemian Forest glacial lakes at altitudes up to 1,079 m (recently known only from
11 Prášílské Lake, Čertovo Lake, and Großer Arbersee; Fig. 1) (Soldán et al. 2012). Our records
12 show the species to be present in Prášílské Lake since at least 8,000 cal. yr. BP, i.e. around the
13 complex multiple erosion episode. *Cyrrnus trimaculatus* is a widely distributed species in
14 flowing as well as in stagnant waters with macrophytes and stony substrate (Graf et al. 2008).
15 It was recorded in historical records from Černé Lake and Großer Arbersee (Klapálek 1903),
16 but more recent records are missing. Larvae of *Philopotamus ludificatus* prefer the epirhithral
17 zone of mountain and submountain streams (Graf et al. 2008). The species is also known from
18 streams in the Bohemian Forest including inflow streams of Prášílské Lake and Laka Lake
19 (Novák 1996; Soldán et al. 2012). *Athripsodes aterrimus* occurs in lakes and pools as well as
20 slow flowing rivers among water plants and on psammopelal habitats (Wallace et al. 1990;
21 Graf et al. 2008). This widely distributed European species occurs also in small pools in the
22 Bohemian Forest at altitudes of ca. 1,000 m a.s.l. (P. Chvojka, unpublished data), but it was
23 not found in any of the glacial lakes recently (Soldán et al. 2012). The *Lype* – *Tinodes*
24 morphotype includes species with an almost concolorous frontoclypeus, e.g. *L. phaeopa* and
25 *T. waeneri*. Both species occur in stagnant and slow flowing waters primarily in lower
26 altitudes. Larvae of *L. phaeopa* live on logs and woody debris while *T. waeneri* prefers stony
27 substrata (Graf et al. 2008). None of the species of Psychomyiidae were recorded from the
28 Bohemian Forest lakes during recent investigations (Soldán et al. 2012), only *L. phaeopa* was
29 found in Großer Arbersee in historical records (Klapálek 1903).

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42 As pH fluctuates annually, seasonally and even daily, the occurring caddisflies are good
43 indicators of the longer-term acidity status of water bodies (Graf et al. 2008). Most of the taxa
44 we identified occur in waters with low pH – only *Philopotamus ludificatus* is moderately
45 sensitive to acidic conditions (Braukmann and Biss 2004; Schartau et al. 2008) – and display
46 a wide range of feeding strategies (Table 3). Some of the species are eurytopic and/or their
47 substrate preferences are ambiguous. In addition, the littoral zone of Prášílské Lake at present
48 is a diverse mosaic of microhabitats and has probably taken this similar form since formation
49 of the lake. Therefore, it is not possible to reconstruct the pattern of changes in the littoral
50 zone substrate through time from our limited caddisfly record. Nevertheless, all dominant taxa
51 found in the sediment core (*Holocentropus dubius*, *Limnephilus* spp., *Agrypnia* – *Phryganea*)
52 inhabit dystrophic water bodies with *Sphagnum* spp. (Graf et al. 2008).

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59 The Early-Holocene caddisfly assemblages (Fig. 3) indicate that the littoral zone of Prášílské
60 lake was partially overgrown by aquatic vegetation (including *Sphagnum* spp.), in

1 combination with muddy and/or sandy substrate. A very similar modern Trichoptera
2 taxocoenoses were found in Laka Lake and Großer Arbersee in this region (Soldán et al.
3 2012), and at Nižné Rakytovské Lake, a small, dystrophic montane lake (1,320 m a.s.l.)
4 further afield in the High Tatra Mts. (Chvojka 1992). Changes between organic and
5 minerogenic sedimentary units usually reflect the alternating stability of catchment hillslopes.
6 During the second phase of the lake evolution (Fig. 3), a series of erosion events occurred
7 between 8,300 and 7,600 cal. yr. BP. This increased transport of allochthonous material
8 documented by the sharp rise in Rb content, may also be reflected in a removal of water insect
9 remains from the shallow to deeper parts of the lake basin. As a result, the highest
10 concentration of frontoclypeal sclerites was recorded in this stratigraphic zone. *Molanna*
11 *nigra* indicate the presence of muddy and sandy substrate but a distinct peak of phytophilous
12 taxa (*H. dubius*, *L. coenosus*-type, *L. rhombicus*-type) suggest a high amount of available
13 plant debris during the same period. This combination of substrates is also in agreement with
14 the ecology of *Cyrnus trimaculatus* (Table 3). The timing of this zone roughly coincides with
15 the establishment of Norway spruce as the most dominant forest canopy taxa in the lake
16 catchment (Carter et al. 2018a), highest biomass burning (Carter et al. 2018b), and the so-
17 called 8.2 ka cooling event (e.g. Tinner and Lotter 2001). However, the series of erosion
18 events in our record lasted around 600 years, while global environmental responses to this
19 climatic event are thought to have lasted no longer than 160 years (Thomas et al. 2007), thus
20 these erosion events cannot be readily linked to the 8.2 ka cooling. In the Middle Holocene,
21 the Trichoptera assemblages were more diverse (8 taxa recorded) and suggest a continuous
22 presence of a more varied littoral zone consisting of macrophytes, mud, sand or gravel.
23 During the Late Holocene, the caddisfly remains were almost absent in the profile implying
24 less favourable conditions for the larvae. The sporadic presence of only one species,
25 *Holocentropus dubius*, was documented until the 20th century when *Agrypnia* – *Phryganea*
26 and both *Limnephilus* morphotypes reappeared again in the record. A low population density
27 could be the cause that the remains did not reach the coring site in the central part of the lake
28 basin in detectable concentrations. However, the period of caddisfly decline begun at the end
29 of the Middle Holocene and approximately coincides with a local European beech (*Fagus*
30 *sylvatica*) expansion into the Norway spruce dominated forest and a dramatic decrease in
31 biomass burning circa 6500 – 500 cal. yr. BP (Carter et al. 2018b). Related changes in leaf
32 litter characteristics (Albers et al. 2004) might have supported near-bottom oxygen depletion.
33 Unfortunately, this lack of subfossil remains therefore does not allow the reconstruction of the
34 pre-acidification trichopteran fauna. It can only be assumed that *H. dubius* was likely to be
35 represented as one of the dominant species. The small increase in number of species and
36 volumetric abundance in the sediment record during the last century (the uppermost part of
37 the Late Holocene zone; Fig. 3) is probably not related to atmospheric acidification and can
38 be explained by other factors. Historical records show that strong gales during the period 1868
39 – 1870 and subsequent active logging destroyed large parts of the forest and increased erosion
40 in the immediate vicinity of Prášilské Lake (Čada et al. 2016). Moreover, the single outflow
41 of the lake was dammed in 1883, raising the lake water level by 2.5 m (Švampera 1914). Both
42 events could have changed the representation of bottom substrate types, oxygen concentration
43 near the bottom or certain hydrological conditions (e.g. water residence time, mixing regime).
44 The pioneer investigations by Šámal (1920) and Novák (1996) document presence of *C.*

1 *villosa*, *M. nigra*, *O. striata* and members of genus *Limnephilus* between 1910s and 1950s.
2 For the same period, we found an evidence of *Agrypnia* – *Phryganea* and both *Limnephilus*
3 morphotypes. This is practically the same assemblage as recorded later in the recovering lake
4 (Soldán et al. 2012).
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7 The subfossil Trichoptera assemblages suggest that Prášílské Lake has been a dystrophic,
8 moderately acid lake from its early development and throughout the Holocene. The species
9 composition shows many similarities to the modern-day ones of Laka and Großer Arbersee
10 lakes (see Soldán et al. 2012). Therefore, the process of natural acidification affected lake
11 water chemistry shortly after the lake formation near the Younger Dryas – Holocene
12 boundary. This is consistent with the timing of Early Holocene lake acidification observed at
13 Kråkenes Lake in Norway (Solem and Birks 2000; Boyle et al. 2013). In the case of Prášílské
14 Lake, however, we are not able to confirm significantly different Late-glacial assemblages.
15 An unexpected absence of a Late-glacial sedimentary record at the study site was confirmed
16 by repeated drilling. This suggests that the onset of lacustrine sedimentation in Prášílské Lake
17 is younger than in other Bohemian Forest lakes. Namely for Černé Lake (Michler 2001),
18 Großer Arbersee (Michler 2000), Plešné Lake (Pražáková et al. 2006), Rachelsee (Carter et al.
19 2018a) and two former lakes (Vočadlova et al. 2015; Kletetschka et al. 2018) the presence of
20 several meters thick Late-glacial sediments is well documented. This asynchrony between
21 timing of local deglaciation (Mentlík et al. 2013) and sedimentation onset in Prášílské Lake
22 may result from a lag time necessary to seal a permeable moraine. Nevertheless, the
23 anticipated Early Holocene onset of natural acidification is supported by evidence from a
24 closely located site, Plešné Lake (Fig. 1), presented by Pražáková et al. (2006) and Kopáček et
25 al. (2009). Their results imply a forest soil development and a subsequent rise in soil organic
26 acids' input to the lake water following the Holocene climatic warming. Both processes are
27 interpreted as key factors leading to dissolved (organically-bound) aluminium increase, pH
28 decrease, oligotrophication, and change in zooplankton species composition. Therefore, we
29 assume that the Early Holocene climatic shift and subsequent changes in vegetation cover
30 triggered natural acidification in the Bohemian Forest region. A future investigation of Late-
31 glacial and Early Holocene sedimentary records might provide further insights into natural
32 acidification history of central European mountain ranges with metamorphic and crystalline
33 bedrock.
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47 **Conclusions**

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50 Here we present, to our knowledge, the first continuous post-glacial records of subfossil
51 caddisfly succession in a mountain lake in central Europe. The results demonstrate signs of
52 natural acidity in the Bohemian Forest region since the Late Pleistocene-Holocene transition.
53 The Prášílské Lake record is characterized by resident caddisfly fauna dominated by species
54 tolerant to low pH (*Holocentropus dubius*, *Limnephilus coenosus*, *L. rhombicus*). Based on
55 our results and the scarce observations from the first half of the 20th century, we conclude that
56 no evidence of a dramatic change in original caddisfly taxocoenoses as a result of the strong
57 anthropogenic acidification was found. The suggested naturally acidic state of the humic lake
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ameliorated the negative effect of changes in water chemistry on macrozoobenthos
community. Our results can be used as a baseline for assessment of biological recovery level
of the study lake in future conservation policies and management. Sediments of glacial lakes
represent crucial natural archives of local post-glacial environmental history that should be
intensively studied. Despite its potential, caddisflies have received less attention from
Quaternary palaeoecologists than many other microfossil groups. Our study underlines the
importance of caddisfly remains as one of the valuable biological proxies in
palaeolimnological research.

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Tables:

Table 1 Results of AMS radiocarbon dating.

Depth (cm)	Core code	Laboratory code	¹⁴ C age (a BP)	Calibrated age (cal. a BP, 2σ range)	Mean calibrated age (cal. a BP)	Material dated
1500.5-1501	Pra-15-2-1	Poz-84783	590±30	494-711	602	Bulk
1539-1539.5	Pra-15-2-1	Poz-81580	2545±30	2422-2782	2631	<i>Picea</i> needle
1628.5-1629	Pra-15-2-1	Poz-87722	7055±40	7763-8317	8009	<i>Picea</i> needle
1571.5-1572	Pra-15-2-2	Poz-81582	4040±35	4223-4812	4506	<i>Picea</i> needles
1599.5-1600	Pra-15-2-2	Poz-81583	5700±40	6198-6677	6469	<i>Picea</i> needle
1628.5-1629	Pra-15-2-2	Poz-80182	7550±40	7763-8317	8009	<i>Picea</i> needles
1637-1637.5	Pra-15-2-2	Poz-87724	7460±40*	8209-8497	8371	<i>Picea</i> needles
1651-1651.5	Pra-15-2-2	Poz-84781	8210±50	8852-9449	9191	<i>Picea</i> needle
1669.5-1670	Pra-15-2-2	Poz-81780	9330±60	10027-10749	10441	<i>Picea</i> bud scales, <i>Betula</i> leaf and seed
1690-1690.5	Pra-15-2-2	Poz-80183	9620±60	10877-11367	11147	<i>Picea</i> seed

* Date excluded by Bacon model.

Table 2 Occurrences of caddisfly larvae (+) documented in Prášilské Lake during the Early Holocene (11,400-8,300 cal. yr. BP), the multiple erosion event (MEE, 8,300 – 7,600 cal. yr. BP), Middle Holocene (7,600 – 4,200 cal. yr. BP), and Late Holocene (4,200 cal. yr. BP – recent). Modern data (1918/1919 – 2015) were compiled by Soldán et al. (2012) and supplemented by 2 additional species (*) observed by J. Petruželová (pers. comm.).

	Early Holocene (11,400 cal. yr. BP – MEE)	Multiple erosion event	Middle Holocene (MEE – 4,200 cal. yr. BP)	Late Holocene (4,200 cal. yr. BP – recent)	1918/1919 – 2015 – lake (modern monitoring)	1918/1919 – 2015 – inflows (modern monitoring)
Family: Rhyacophilidae						
<i>Phyacophila glareosa</i> McLachlan, 1867						+
<i>Rhyacophila praemorsa</i> McLachlan, 1879						+
Family: Philopotamidae						
<i>Philopotamus ludificatus</i> McLachlan, 1878			+			+
Family: Polycentropodidae						
<i>Cymus trimaculatus</i> (Curtis, 1834)	+	+	+			
<i>Holocentropus dubius</i> (Rambur, 1842)	+	+	+	+	+	*
<i>Plectrocnemia conspersa</i> (Curtis, 1834)					+	+
<i>Plectrocnemia geniculata</i> McLachlan, 1871						+
Family: Psychomyiidae						
Lype – Tinodes			+			
Family: Phryganeidae						
<i>Agrypnia varia</i> (Fabricius, 1793)					+	
<i>Agrypnia – Phryganea</i>	+		+	+		
<i>Oligotricha striata</i> (Linnaeus, 1758)	+				+	
<i>Phryganea bipunctata</i> Retzius, 1783					+	
Family: Apataniidae						
<i>Apatania fimbriata</i> (Pictet, 1834)						+
Family: Limnephilidae						
<i>Drusus annulatus</i> (Stephens, 1837)						+
<i>Drusus discolor</i> (Rambur, 1842)						+
<i>Limnephilus centralis</i> Curtis, 1834					+	
<i>Limnephilus coenosus</i> -type	+	+		+	+	*
<i>Limnephilus lunatus</i> Curtis, 1834					+	
<i>Limnephilus rhombicus</i> (Linnaeus, 1758)					+	
<i>Limnephilus rhombicus</i> -type	+	+	+	+		
<i>Chaetopteryx villosa</i> (Fabricius, 1798)					+	+
<i>Pseudopsilopteryx zimmeri</i> (McLachlan, 1876)						+
<i>Psilopteryx psorosa bohemosaxonica</i> Mey et Botosaneanu, 1985						+
<i>Parachiona picicornis</i> (Pictet, 1834)						+
Family: Molannidae						
<i>Molanna nigra</i> (Zetterstedt, 1840)		+	+		+	
Family: Leptoceridae						
<i>Athripsodes aterrimus</i> (Stephens, 1836)			+			

Table 3 Caddisfly taxa and morpho-taxa documented in the sediment record from Prášilské Lake and their feeding strategies and habitat, substrate and pH preferences. For the morpho-taxa which most likely belong to a particular species (*), we present ecological characteristics of a such species.

Taxon	Functional feeding group	Habitat	Substrate	Sensitivity to acid water	References
<i>Agrypnia - Phryganea</i>	gat, pre, shr	L	alg, mph, pel, pom, woo	-	Graf et al. (2008)
<i>Athripsodes aterrimus</i> (Stephens, 1836)	gat, pre, shr	L, S	mph, pel, psa	IN	Fjellheim and Raddum (1990), Graf et al. (2008), Schartau et al. (2008)
<i>Cyrnus trimaculatus</i> (Curtis, 1834)	pff, pre	L, S	mal, mil, mph	IN	Fjellheim and Raddum (1990), Graf et al. (2008)
<i>Holocentropus dubius</i> (Rambur, 1842)	pff, pre	L	mph	IN	Fjellheim and Raddum (1990), Graf et al. (2008), Schartau et al. (2008)
* <i>Limnephilus coenosus</i> Curtis, 1834	gra, pre, shr	L	pel, mph, pom, psa	AR	Zamora-Muñoz and Svensson (1996), Krno et al. (2006), Graf et al. (2008)
* <i>Limnephilus rhombicus</i> (Linnaeus, 1758)	gra, pre, shr	L, S	pel, mph, pom, psa	AR	Fjellheim and Raddum (1990), Braukmann and Biss (2004), Graf et al. (2008)
* <i>Lype phaeopa</i> (Stephens, 1836)	gra, xyl	L, S	woo	AS?	Graf et al. (2008)
<i>Molanna nigra</i> (Zetterstedt, 1840)	gat, pre	L	pel, psa	IN?	Graf et al. (2008), Soldán et al. (2012)
<i>Oligotricha striata</i> (Linnaeus, 1758)	gat, pre, shr	L	mal, mph, pel, pom, psa	AT	Wallace et al. (1990), Braukmann and Biss (2004), Graf et al. (2008)
<i>Philopotamus ludificatus</i> McLachlan, 1878	pff	S	mal, mil	AS	Braukmann and Biss (2004), Graf et al. (2008)
* <i>Tinodes waeneri</i> (Linnaeus, 1758)	gat, gra, pff, pre	L, S	mal, mil	IN	Fjellheim and Raddum (1990), Graf et al. (2008), Ings et al. (2017)

Functional feeding groups: gat – gatherer/collector, gra – grazer and scraper, pff – passive filter feeder, pre – predator, shr – shredder, xyl – xylophage.

Substrate preference: alg – algae, mal – stones and bedrock, mil – coarse gravel (2 – 20 cm), mph – macrophytes and mosses, pel – mud, pom – coarse and fine particulate organic matter, psa – sand, woo – woody debris.

Habitat: L – lake (littoral and/or sublittoral zone), S – stream.

Sensitivity to acidification: AR – acid resistant (pH < 5.5), AS – moderately acid sensitive (pH around 6.5 – 7.0), AT – acid tolerant (pH 6.5 – 5.5 and sometimes bellow), IN – indifferent (occurrence across wide range of pH including values < 5.5).

Figures:

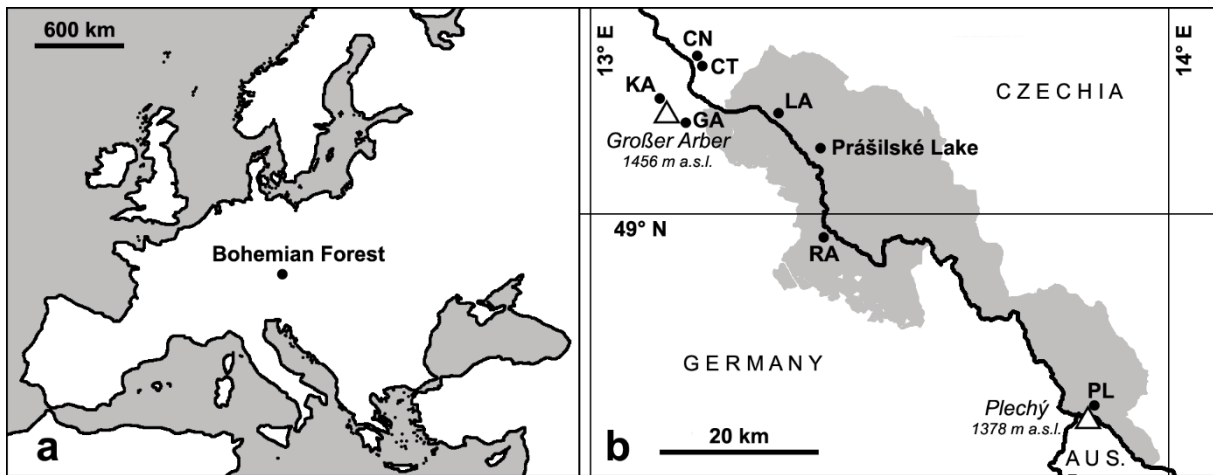


Figure 1 Location of the Bohemian Forest in Europe (a). Location of the study site (Prášílské Lake) within the Bohemian Forest lake district (b). Area of Šumava National Park, Czechia, and Bayerischer Wald National Park, Germany, is shown in grey. Depicted are the tallest mountains of the two national parks, as well as all 8 glacial lakes. LA = Laka Lake; CT = Čertovo Lake; CN = Černé Lake; KA = Kleiner Arbersee; GA = Großer Arbersee; RA = Rachelsee; PL = Plešné Lake.

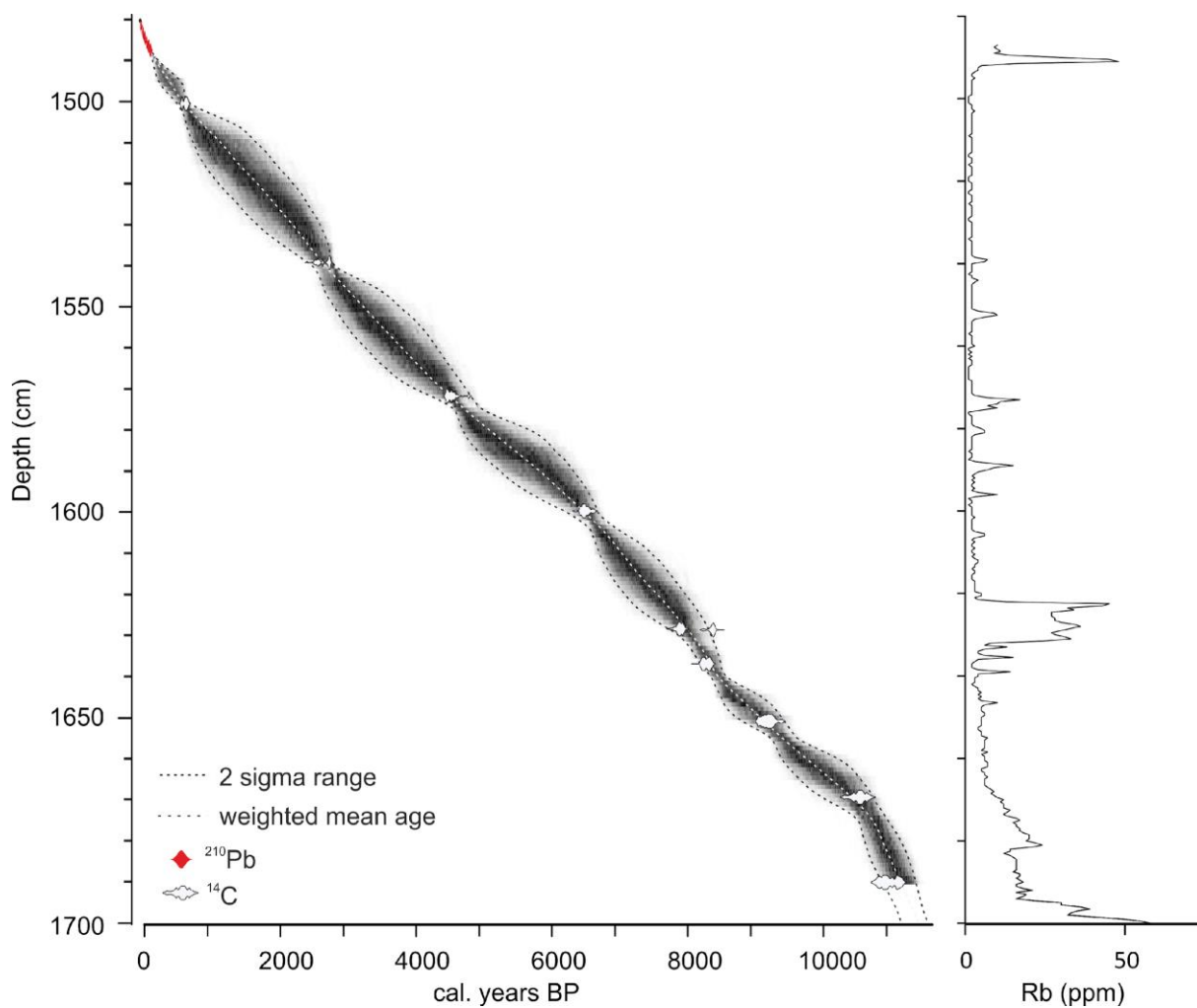


Figure 2 Bayesian age-depth model and rubidium (Rb) concentrations for Prášílské Lake sediment profile (core drives PRA15-GC-2, PRA15-1-2, PRA15-2-1, and PRA15-2-2).

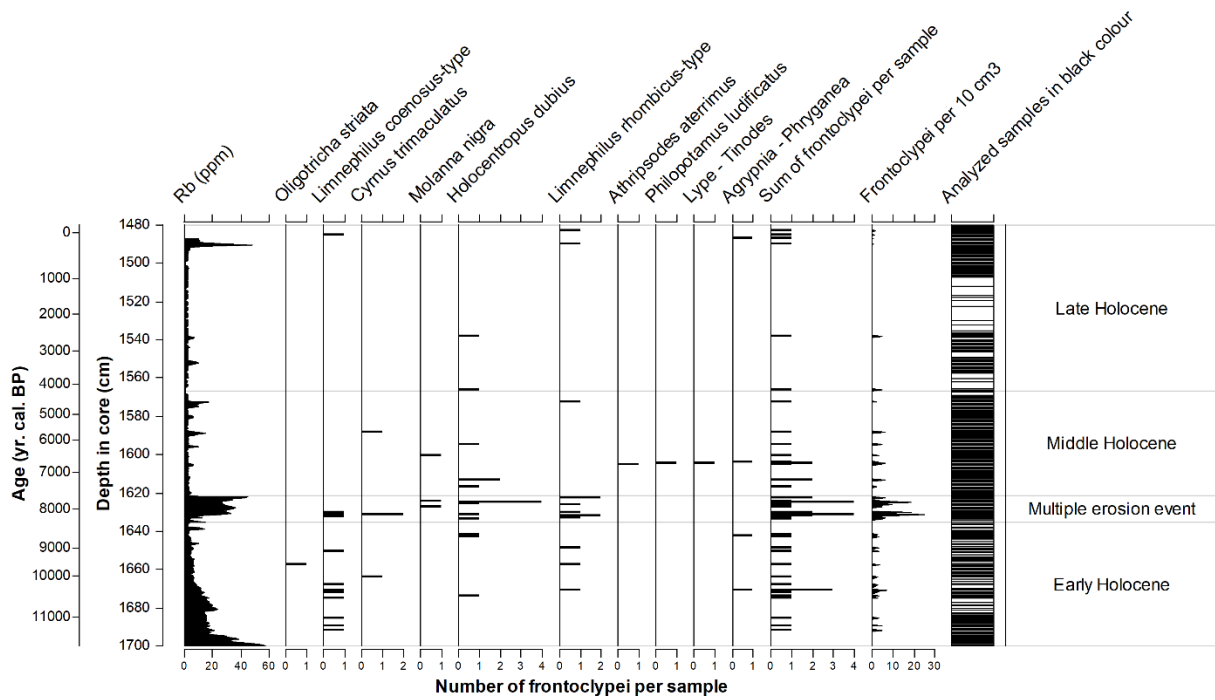


Figure 3 Changes in caddisfly assemblages in Prášilské Lake through time. The core runs from the top of the sediment at 1480 cm water depth to the sandy substrate at 1699 cm. Increases in rubidium (Rb) demonstrate periods of erosional activity in the lake watershed. The four zones were added according to the division of the Holocene epoch (Walker et al. 2012), with an additional zone represented by a multiple erosion event between the depth of 1634.5 cm and 1621.5 cm (8,300 – 7,600 cal. yr. BP).

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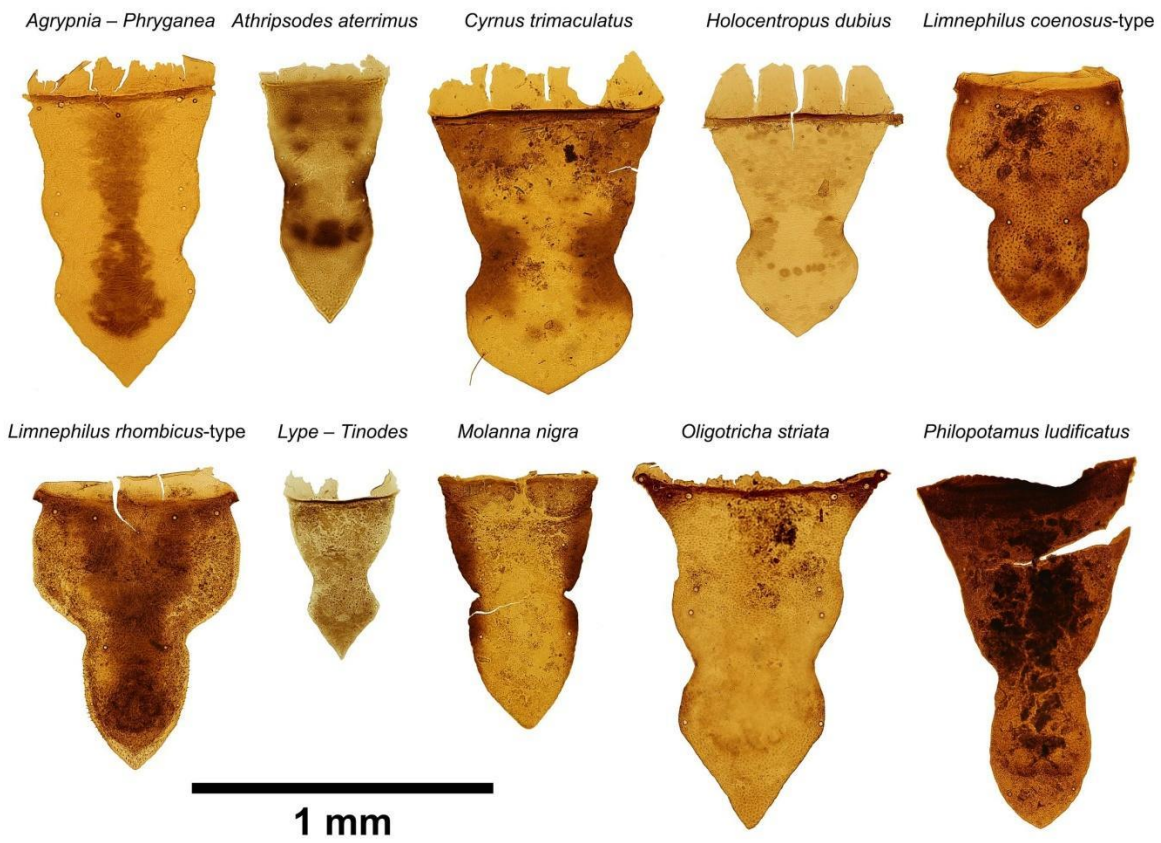


Figure 4 Frontoclypeal apotomes of all caddisfly taxa found in this study.