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Holocene tree immigration and the chironomid fauna of a small Swiss subalpine lake (Hinterburgsee, 1515 m asl)

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Abstract

Early Holocene reforestation by stone pine (*Pinus cembra*) and tree birch (*Betula pubescens*) took place ca. 500 years after the end of the Younger Dryas at Hinterburgsee, a small subalpine lake in the northern Swiss Alps. During the next ca. 3000 years the local vegetation consisted of open woodlands with many pioneer dwarf shrubs and herbs. The expansion of silver fir (*Abies alba*) at ca. 7400 calibrated radiocarbon years before present (cal. BP) and Norway spruce (*Picea abies*) at ca. 6000 cal. BP in Hinterburgsee's catchment led to a closing of the local forests with a successive decrease in erosion and a distinct change in Hinterburgsee's sediment composition. First signs of probably human-induced openings of the catchment forest are apparent at ca. 2500 cal. BP, but it is not until the past ca. 800 years that pollen analysis suggests strong local and regional anthropogenic activity. The strongest and most abrupt changes in the Holocene development of Hinterburgsee's chironomid fauna took place at ca. 11 500 cal. BP and at ca. 10 000 cal. BP, when parts of the alpine taxa that were dominant during the Younger Dryas disappeared from the lake. The first change is most likely related to the increasing temperatures after the end of the Younger Dryas, the second possibly to decreasing lake depth and increasing summer insolation in the early Holocene that may have led to warmer bottom water temperatures in the lake. No clear relationship between the changes in catchment vegetation and the development of the chironomid fauna was found. Possibly the increase in sediment organic matter associated with the denser catchment forests was responsible for a succession in the chironomid stratigraphy between 7000 and 4500 cal. BP. However, due to the high sedimentation rates in Hinterburgsee this trend could also be a consequence of, or be promoted by, the sediment infilling of the lake basin. This conjecture is supported by the increasing importance of *Tanytarsus lugens*-type, a chironomid taxon dominant in the extant chironomid assemblages of shallow mountain lakes in Switzerland. The only shift in the chironomid fauna that clearly parallels a change in catchment vegetation is found during the past ca. 800 years. We discuss possible reasons for the comparatively weak influence of catchment vegetation on the chironomid fauna of Hinterburgsee and the implications of our results for multi-proxy studies on past climate involving both palaeobotanical and chironomid-based reconstructions.

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1. Introduction

The Holocene period is receiving increasing attention by palaeoecologists and palaeolimnologists because human-induced changes on terrestrial and limnic ecosystems can only be assessed in relation to the natural, millennium-scale dynamics of these systems before the onset of anthropogenic influence (e.g. Anderson and Battacharya, 1994; Itkonen et al., 1999; Lotter, 2001). Furthermore, Holocene palaeoclimate reconstructions are necessary in order to examine the natural climate variability, the relationship of climate to possible forcing mechanisms and to understand the significance and causes of the global warming trend during the past century (Bradley, 2000).

Small mountain lakes in the Alpine region provide an interesting setting for studies of past vegetation, limnology, and climate. The steep catchment topography often leads to high allochthonous sediment input and therefore to high sedimentation rates. Thus, the sediments in these lakes provide high-resolution archives for palaeoecological and palaeoclimatological studies. If the lakes are situated in the lower alpine or subalpine vegetation zone, palaeobotanical studies can provide insights to changes in past timberline elevation. As temperature is one of the factors limiting tree growth at alpine timberlines (Tranquillini, 1979), the reconstruction of former tree-line altitude offers information on past climate (e.g. Burga, 1993; Wick and Tinner, 1997). Major tree immigration paths into the Alpine region can be inferred, providing information of interest to biogeography and plant ecology. Furthermore, subfossil assemblages of aquatic organisms can be studied in the same sediment as the palaeobotanical proxies. A survey of the remains of diatoms, chrysophyte cysts, cladocera and chironomids in the surface sediments of small Swiss lakes suggests that in the Alps subfossil assemblages in lakes just below the present-day timberline are exceptionally sensitive to temperature changes (Lotter et al., 1997a). The distribution of some of these, e.g. the remains of chironomid larvae (Insecta: Diptera: Chironomidae), is strongly related to summer temperature (Walker et al., 1991b; Lotter et al., 1997a; Olander et al.,

1999) and they can thus be used to model quantitatively past air or water temperatures (e.g. Walker et al., 1991a; Levesque et al., 1993). Therefore, besides providing background information on the long-term development of lake ecosystems, Holocene chironomid stratigraphies can provide an additional estimate of past climate change. Finally, instrumental records indicate that changes in climate in the Alps may be more distinct at high elevations than in the lowlands (Beniston et al., 1997). Thus, palaeoclimatological studies in alpine and subalpine lakes may pick up temperature signals that are too weak to affect terrestrial or aquatic ecosystems at lower altitudes.

A number of multi-proxy studies with a focus on reconstructing past climate have recently been implemented in the Alpine region (e.g. Ammann, 2000; Lotter et al., 2000; Lotter and Birks, accepted). They combine information on former terrestrial vegetation and aquatic lake biota to produce more reliable environmental reconstructions than would be possible in single-proxy studies. *Sensu stricto* quantitative organism-based inference models assume that environmental variables other than the parameter of interest have a negligible influence on fossil assemblages during the period of reconstruction (Birks, 1995). However, in polar regions there is a distinct change in lake water chemistry across the tundra-boreal forest ecotone (e.g. Anderson, 2000; Smol and Cumming, 2000). In addition, palaeolimnological evidence suggests that in more temperate regions the immigration of new tree species into a lake's catchment can significantly affect lake water chemistry and thereby phytoplankton assemblages (e.g. Korsman et al., 1994). For chironomids a change of assemblage composition with the arctic tree-line has been reported (Walker and MacDonald, 1995; Porinchu and Cwynar, 2000). In the Alps, limnological changes associated with the treeline ecotone seem to be less pronounced (Lotter et al., 1997a, 1998; Müller et al., 1998). Nevertheless, when reconstructing past temperatures using quantitative inference models based on chironomids, changes in the catchment vegetation may possibly be responsible for shifts in the chironomid assemblages. There exists, therefore, the danger of cir-

cular argumentation when using palaeobotanical data to support quantitative chironomid-based temperature reconstructions from the same sediment or vice versa. This is particularly a problem for the Holocene, as anticipated temperature changes are small and local artefacts may be more difficult to separate from the climate signal than during periods with more pronounced climate changes.

Here we present the results of a multi-proxy Holocene study of Hinterburgsee, a small lake in the subalpine zone of the Swiss Alps. Pollen and plant macrofossil analysis is used to describe the vegetation history in Hinterburgsee's catchment. Furthermore, a chironomid stratigraphy from Hinterburgsee is presented and major trends in the long-term development in the chironomid assemblages are discussed. Finally, as the lake's catchment has experienced distinct shifts in vegetation, the vegetation history is compared to changes in the chironomid fauna to assess if catchment vegetation development is a major factor affecting the chironomid assemblages.

2. Study site

Hinterburgsee is a small mountain lake situated at 1515 m asl on calcareous bedrock in the northern Swiss Alps (8°4'03"E, 46°43'06"N). It is located above the southern shore of Lake Brienz, ca. 16 km east of Interlaken and 4.5 km south to southeast of Brienz (Fig. 1A). Parts of the catchment above the southern lake shore consist of a precipice, whereas the remaining slopes show a more gentle incline. Hinterburgsee has one major tributary on the western shore that is active mainly during spring. The lake is drained by a sinkhole on the northern shore (Fig. 1B). Due to the lake's constant water level and outflow it is assumed that part of the water inflow takes place subterraneously (Guthruf et al., 1999). The lake has a major basin with a maximum depth of 11.1 m and a minor basin in the eastern part (Fig. 1B). The surrounding vegetation consists mainly of Norway spruce (*Picea abies*) and, especially on the steep southern slopes, of green alder (*Alnus viridis*). Bare rock in the form of cliffs on the

southern precipice and as boulders and blocks on the other slopes makes up ca. 15% of the total catchment. Several meadows and parts of the open woodlands are used for summer pasturing (Spengler, 1973). Lake water chemistry measurements indicate meso- to eutrophic conditions in the lake today with 33 µg total phosphorus l⁻¹ and 1.16 mg total nitrogen l⁻¹ (averaged over the whole water column). Hinterburgsee generally freezes from mid-October to mid-November and thaws around mid-May (Spengler, 1973).

3. Methods

In August 1997, two parallel cores were taken in the deepest part of the lake (Fig. 1B) using a modified 8-cm-diameter Livingstone piston corer (Merkt and Streif, 1970; Lotter et al., 1997b). The two cores were taken within a horizontal distance of 1 m and with a vertical offset of 50 cm (henceforth referred to as core A and core B). A gravity corer (Renberg, 1991) was used to sample the top-most 60 cm of water-saturated sediment. The core segments of 1 m length were extruded from the stainless steel tubes on site and transported to the laboratory, where they were lengthwise cut into halves using two copper sheets. The sheets were inserted into the sediment cores laterally and the two core halves separated, each with one copper sheet covering the freshly cut sediment. After the cores had been photographed, described lithologically and correlated, one half core of the sequence was contiguously sampled for different analyses, the other half stored as reference.

Loss-on-ignition (LOI) analyses were carried out on 1-cm³ samples of sediment and in approximately 10-cm intervals following the recommendations in Heiri et al. (2001) (i.e. 4 h of combustion at 550°C for the estimate of organic matter content and 2 h at 950°C for the estimate of carbonate content). For pollen analysis 1 cm³ of sediment was prepared using standard methods with 10% KOH, 10% HCl, 40% hydrofluoric acid (HF) and acetolysis (see Fægri and Iversen, 1989), mounted in glycerine and identified under a compound microscope at 1000× magnification (average count sum: 500 pollen grains per sam-

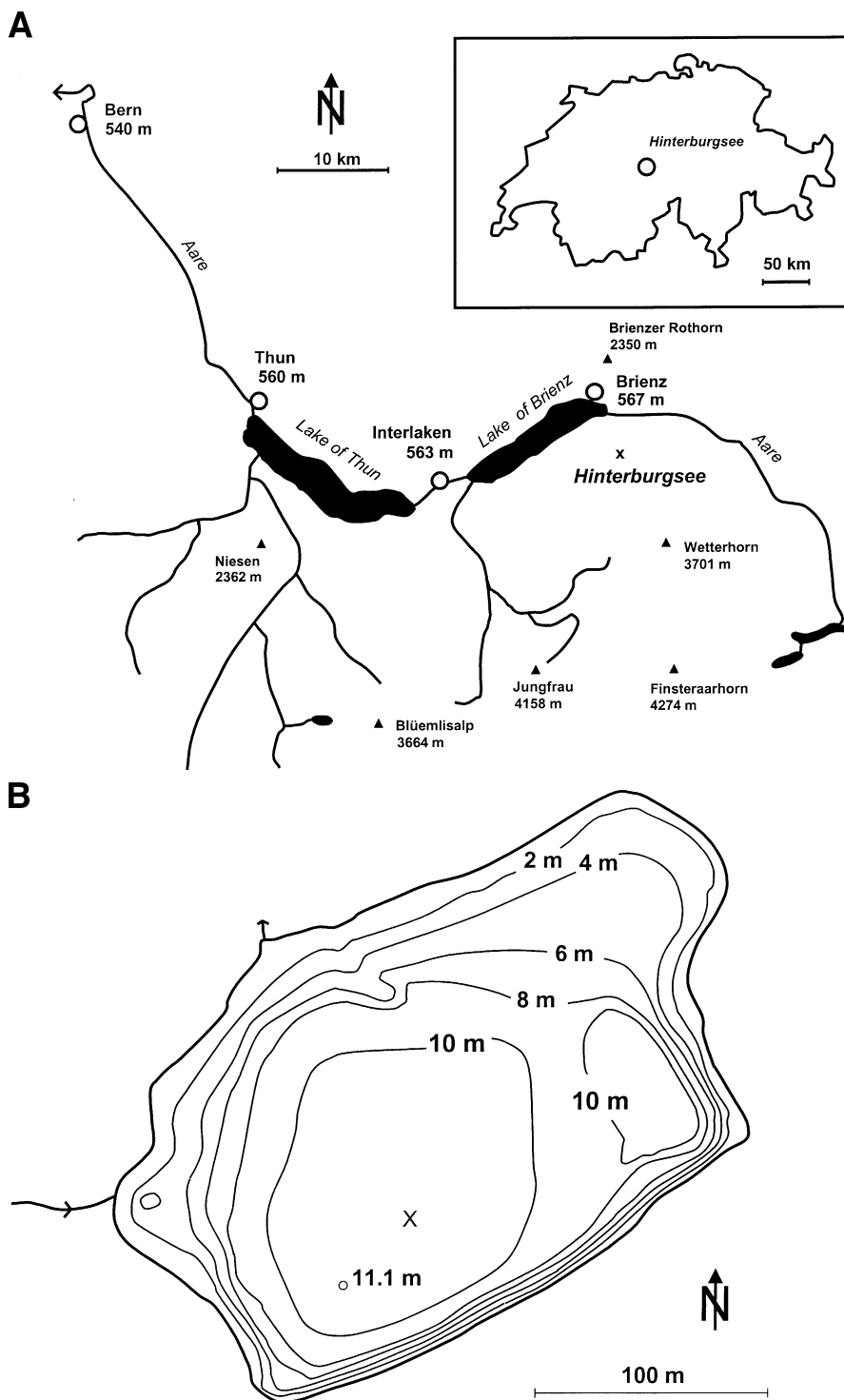


Fig. 1. (A) Location of Hinterburgsee in the Bernese Alps (detailed map) and within Switzerland (inset map). (B) Bathymetry of Hinterburgsee (following Spengler, 1973, changed). The open circle indicates the deepest part of the lake basin and the × the coring site.

ple). Pollen percentages were calculated excluding aquatic plant pollen from the total pollen sum. For plant macrofossil and chironomid analysis, sediment slices of 2 cm thickness and ca. 30–40 cm³ volume were immersed in 5% KOH for 2–3 h and subsequently sieved through a 200- μ m and a 100- μ m sieve. The 200- μ m fraction was examined for plant macrofossils and charcoal under a stereomicroscope and large terrestrial plant remains were set aside for radiocarbon dating. After joining the 200- μ m and 100- μ m fractions the residue was examined for subfossil chironomids. Due to the minerogenic nature of the sediment, chemical treatment of the residue with HF was necessary to eliminate the inorganic sediment components (see Walker and Mathewes, 1989). Head capsule concentrations were very variable and therefore a modified two-chamber subsampler (Meyer, 1990) was used to reduce the size of some samples before picking the chironomid remains at 35 \times magnification under a stereomicroscope. Chironomids were mounted in Euparal[®] mounting medium after dehydration and identified at 100 \times and 400 \times magnification with a compound microscope. Taxonomy mainly follows Hofmann (1971), Wiederholm (1983), Schmid (1993) and Rieradevall and Brooks (2001). The identification of *Micropsectra* spp., *Micropsectra radialis*-, *Corynoneura scutellata*- and *Tanytarsus lugens*-type is described in detail in Heiri (2001) and of *Tanytarsus* A, *Cricotopus*- and *Orthocladius*-type in Lotter et al. (1997a). *Psectrocladius* (*s.str.*) includes all *Psectrocladius* head capsules not of a *Psectrocladius* (*Allopectrocladius*)- or *Psectrocladius* (*Mesopsectrocladius*)-type as described in Wiederholm (1983). *Paratanytarsus* spp. contain all *Paratanytarsus* except *Paratanytarsus austriacus*-type (i.e. all without the combination of a pigmented head capsule and three inner teeth on the mandible). Finally, *Zavrelimyia* A has dorsal head capsule pores that, instead of forming almost a right angle as described for *Zavrelimyia punctatissima* in Rieradevall and Brooks (2001), are arranged in a curved row, forming a broader angle (ca. 120°).

Besides larval head capsules, two types of respiratory organs (thoracic horns) of pupae of the genus *Procladius* were isolated from the sediment.

Procladius type 1 pupae feature an elongate thoracic horn with a length to width ratio of 3.7 to 4.1 ($n=5$), with the widest part in the middle of the horn (e.g. as described for *Procladius choreus* or *Procladius signatus* in Langton, 1991). *Procladius* type 2 thoracic horns, on the other hand, were flattened as described for '*Procladius tatrensis*' in Gowin and Zavrel (1944) with a length to width ratio of 2.0 to 2.3.

Detrended correspondence analysis (DCA) was carried out using the program CANOCO version 4.0 (ter Braak and Smilauer, 1998) and using untransformed percentage data and downweighting of rare species. The partitioning of the stratigraphies into assemblage zones was accomplished by eye.

4. Results

4.1. Lithology

Sediment to 1280 cm below the sediment/water interface was obtained from both cores A and B. It was not possible to acquire deeper sediment from core A. Core B reached to a depth of 1575 cm below the sediment/water interface, where further penetration of the corer was impeded by a gravel layer of at least 24 cm thickness. The sediment cores were correlated using lithological features (turbidites, slumps and sand layers) to produce a continuous sediment sequence down to a depth of 1280 cm below the sediment/water interface. As the corresponding sequences of core A are not available for the lowermost sediments there are two hiatus of approximately 10 cm thickness between the last three core segments of core B (Fig. 2a).

A total of 30% of the Hinterburgsee deposits consist of turbidites, slumps or sand layers. As such sequences represent single, abrupt sedimentation events and tend to incorporate reworked organic material, they disturb the chronological order of the sediment and can seriously bias stratigraphic analyses of organic remains and age–depth relationships. Therefore, except where otherwise indicated all references to sediment depth henceforth refer to a corrected sediment

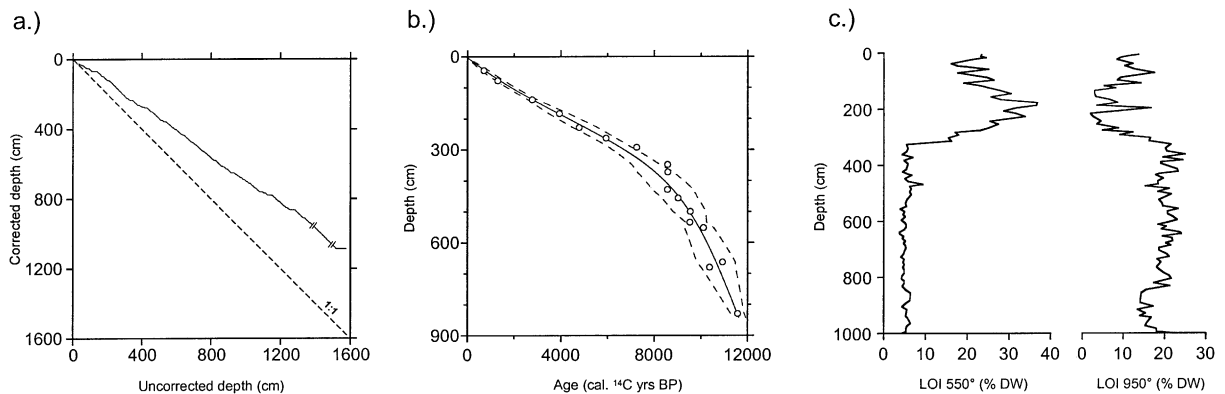


Fig. 2. (a) Relationship between corrected and uncorrected sediment depth in the Hinterburgsee core (solid line). The uncorrected depth is the core depth from the water/sediment interface, whereas for the corrected depth the turbidites and slumps were excluded. The interruptions in the curve indicate two hiatus of ca. 10 cm thickness. (b) Dating of the Hinterburgsee core: age–depth model (solid line) and 95% confidence intervals (dotted lines). Circles indicate the calibrated dates used for the model (see Table 1). The sediment depth is plotted in corrected values (see text for details). (c) LOI as % dry weight (DW) measured in the Hinterburgsee sediment. The sediment depth is plotted in corrected values (see text for details).

depth that excludes turbidites, slumps and sand layers (see Fig. 2a).

According to lithological characteristics, the sediment sequence can be roughly separated into two parts. Below ca. 310 cm sediment depth the deposits are highly minerogenic, with a low organic and high carbonate content (Fig. 2c). They consist of silty clays with intercalated sandy layers. The lacustrine sedimentation is interrupted by numerous slumps and turbidites ranging from a few millimetres up to 30 cm thickness. From a sediment depth of about 310 cm to the core top, the sediment consists of a calcareous fine-detritus gyttia (Fig. 2c). Again, the sediment features numerous turbidites and slumps in the same size range as in the lower part of the core. Furthermore, a number of thin (< 1 cm) layers of woody debris and other coarse organic detritus were identified upon visual inspection.

4.2. Chronology

A total of 17 samples was AMS-radiocarbon dated, seven of which originate from slumps or turbidites (Table 1). The core top (–47 cal. BP) and the Younger Dryas/Holocene boundary (10 000 uncalibrated radiocarbon years BP, see results of pollen analysis for details) provided two further dates. One of the radiocarbon dates

from a slump was excluded from the age–depth model as it was obviously too old compared to the other dates in the sequence (Ua-13,348; Table 1). The remaining 18 dates were converted to calibrated radiocarbon years before present using method A in the CALIB 4.1.2 program (Stuiver and Reimer, 1993). Age–depth modelling was accomplished using non-parametric weighted regression within the framework of generalised additive models (see Lotter and Birks, accepted, for details on the method). Both the core top and the Younger Dryas/Holocene boundary were forced by giving these dates significantly more weight than the radiocarbon dates. The simplest, parsimonious age–depth model was based on a variance function proportional to the mean and a four degrees of freedom equivalent smoothing parameter. For the final age–depth model, ages were estimated by interpolation for every centimetre and the 95% confidence interval calculated for each depth (Fig. 2b). Henceforth, all references to ages are given in these estimated calibrated radiocarbon ages (abbreviated as cal. BP). As the oldest date in the Hinterburgsee core is at ca. 11 500 cal. BP, the older sediment remains undated. For graphical representation a constant sedimentation rate of 5.3 yr cm^{–1} is assumed for Late Glacial sediments (i.e. the same sedimentation rate as calculated for the oldest Holocene sediments).

Table 1
Dates used for the Hinterburgsee age–depth model

Sample/laboratory No.	Depth (cm)	Uncal. ¹⁴ C years BP	S.D.	Cal. ¹⁴ C years BP	Remarks
Core top	0	–47	-	–47	Sediment/water interface
Ua-14,630	45	805	± 60	701	–
Ua-14,631	78	1 425	± 60	1 306	Possibly slump
Ua-14,632	138	2 665	± 65	2 760	–
Ua-13,347	183	3 625	± 65	3 919	–
Ua-13,642	226	4 215	± 95	4 767	–
Ua-14,633	262	5 145	± 80	5 912	Slump
Ua-13,348	277	8 000	± 90	8 874	Slump, excluded from age–depth model
Ua-14,634	290	6 375	± 95	7 235	Detritus
Ua-14,635	347	7 835	± 90	8 555	Turbidite
Ua-14,636	371	7 880	± 80	8 578	–
Ua-13,643	427	7 835	± 140	8 555	Slump
Ua-14,637	454	8 105	± 85	8 988	–
Ua-13,644	498	8 660	± 110	9 538	–
Ua-14,638	534	8 560	± 85	9 492	Turbidite
Ua-13,349	552	9 190	± 80	10 086	Wood layer/detritus
Ua-13,350	664	9 635	± 95	10 892	Turbidite
Ua-13,645	678	9 370	± 115	10 359	Turbidite
Younger Dryas/Holocene boundary	826	10 000	-	11 550	Pollen-inferred age

All depth values are in the corrected depth scale (see text for details).

4.3. Pollen

The deepest pollen samples retrieved from Hinterburgsee show a flora typical of Swiss Late Glacial sediments, with a high percentage of *Pinus* (subgenus *Pinus*), *Betula*, Gramineae, and *Artemisia* pollen (pollen assemblage zone (PAZ)-1; Fig. 3). The dominance of *Pinus* pollen and high *Artemisia* percentages indicate that the whole Late Glacial sediment sequence (before 11 500 cal. BP) originates from the Younger Dryas biozone (Wegmüller and Lotter, 1990; Wick, 2000). The decline in Gramineae and *Artemisia* pollen and the increase in *Pinus cembra* mark the Late Glacial/Holocene boundary (e.g. Wick and Tinner, 1997; Wick, 2000). The Holocene palynostratigraphy is dominated by the typical sequence of tree immigrations known from other Holocene sediment sequences from the Swiss Plateau and the Northern Swiss Alps (e.g. Ammann et al., 1996; van der Knaap and Ammann, 1997). During PAZ-2, *Pinus cembra* is joined by *Corylus avellana*, *Ulmus*, *Tilia*, *Quercus* and *Alnus glutinosa*-

type. At the end of PAZ-3 (ca. 7500 cal. BP), *Abies* percentages increase, later followed by *Picea*, *Fagus* and *Alnus viridis* during PAZ-4 and 5. The younger sediments of Hinterburgsee indicate increasing human activity near the lake. *Plantago lanceolata*-type appears at ca. 4000 cal. BP, later followed by a gradual increase of Gramineae and successive increases of other grazing and culture indicators such as *Rumex acetosa*-type, *Rumex alpinus*, *Plantago alpina*-type and *Urtica*. These pollen types are commonly associated with pasturing and feature the highest percentages in PAZ-6 (i.e. in the last ca. 800 years). Furthermore, the Hinterburgsee stratigraphy shows relatively high values of pollen and spores from plants indicating open woodlands or soil instability (e.g. Monolete fern spores, *Dryopteris filix-mas*-type, *Pteridium aquilinum*, *Athyrium filix-femina*, *Selaginella selaginoides*).

4.4. Plant macrofossils

The Late Glacial and earliest Holocene sedi-

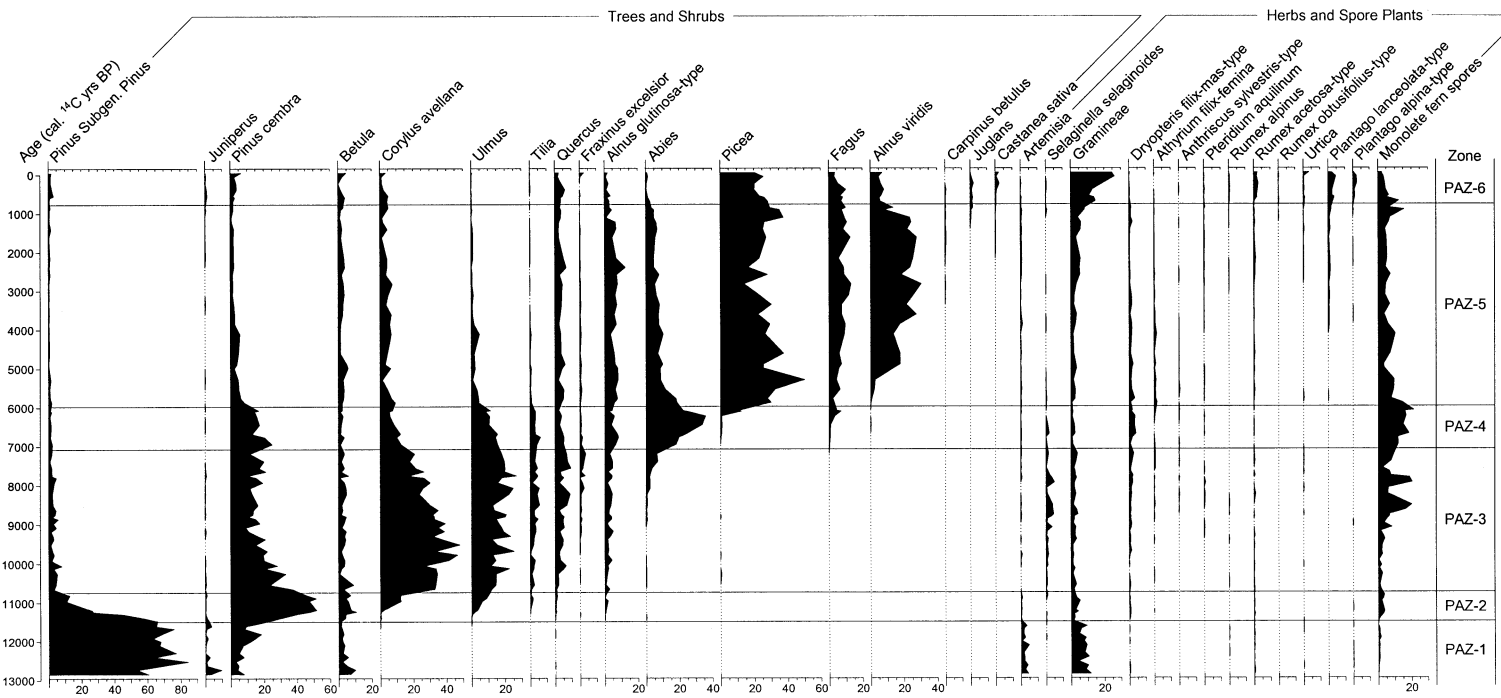


Fig. 3. Pollen stratigraphy of Hinterburgsee (values in percentages of total terrestrial pollen). Only selected pollen types are shown.

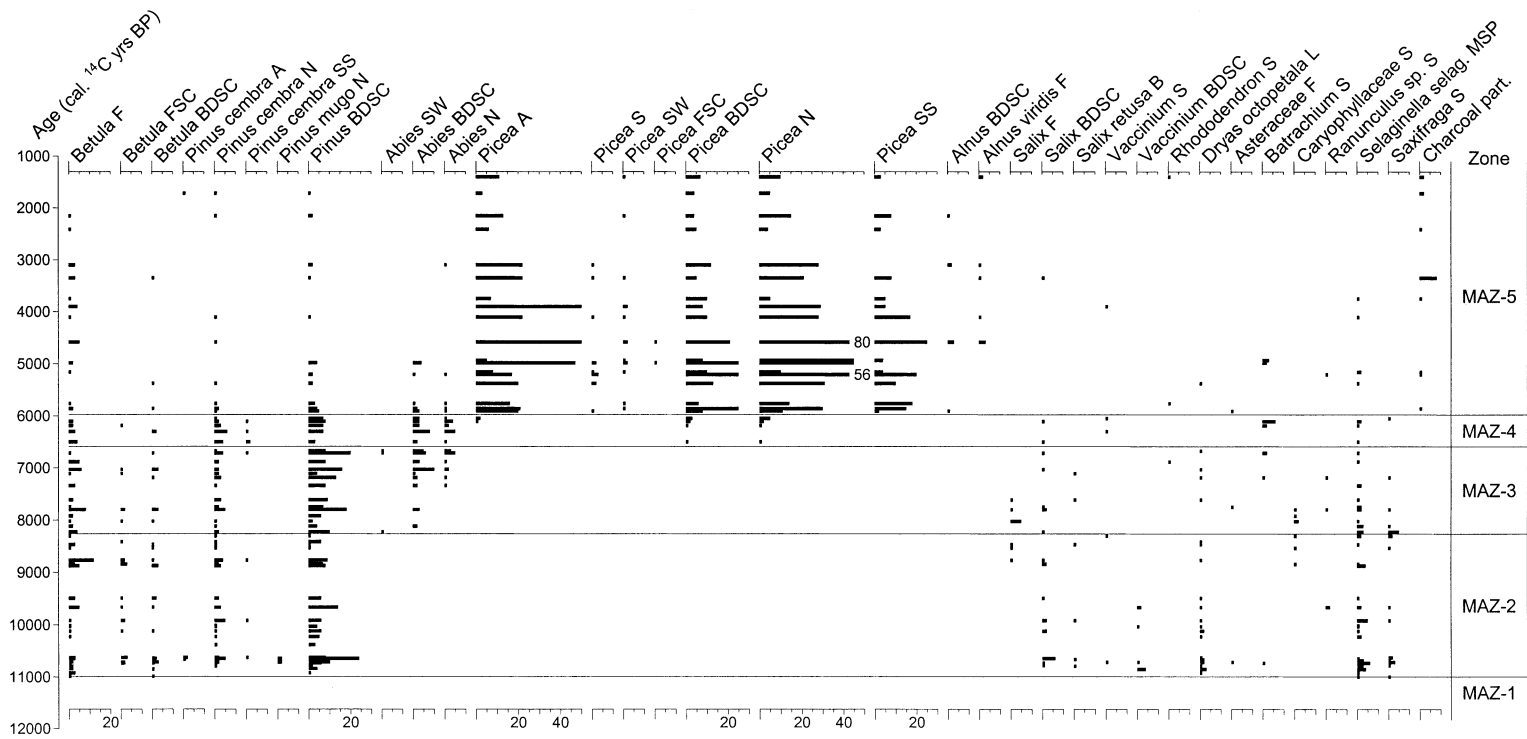


Fig. 4. Plant macrofossils of selected taxa found in the Hinterburgsee sediment. Values are in remains per 30–40 cm³ sample volume for anthers (A), bud scales (BDSC), fruits (F), fruit scales (FSC), leaves (L), macrospores (MSP), needles (N), seeds (S), short shoots (SS), and seed wings (SW). Periderm, wood and fragments with less than three occurrences are not shown. No samples younger than 1300 cal. BP were analysed.

ments of Hinterburgsee before 11 000 cal. BP contained hardly any plant macrofossils (macrofossil assemblage zone (MAZ)-1; Fig. 4). After ca. 11 000 cal. BP the first macrofossils of *Betula*, *Pinus cembra* and *Pinus mugo* were found. Remains of these three trees, together with remains of heliophilous herbs and shrubs (e.g. *Salix retusa*, *Dryas octopetala*, *Selaginella selaginoides* and *Saxifraga*), remained abundant in the sediment of Hinterburgsee until ca. 5000–6000 cal. BP (MAZ-2, 3, 4). A number of *Betula* remains were identifiable as belonging to *Betula pubescens*. At ca. 8200 cal. BP the first bud scales of *Abies* were found. However, it takes another ca. 700 years until a significant increase of *Abies* macrofossils is apparent in the sediment. A strong increase in *Picea* macrofossils is apparent around 6000 cal. BP, about 500 years after the first remains were found in the sediments. At the same time the remains of dwarf shrubs and herbs become sparse. After reaching maximum values at the beginning of MAZ-5 (between ca. 5500 and 4000 cal. BP) the abundance of *Picea* macrofossils decreases again. Compared to the high percentages of *Alnus viridis* in the pollen stratigraphy, *Alnus* macrofossils were sparse in the Hinterburgsee sediment. However, this may be explained by the generally poor preservation of *Alnus viridis* remains in lake sediments. The first macroscopic charcoal remains were found in Hinterburgsee at ca. 5800 cal. BP, just after the expansion of *Picea* in the catchment. Additional charcoal was found in younger sediments, although with no clear maximum. The absence of macrofossils of *Corylus*, *Ulmus*, *Tilia*, *Quercus* and *Alnus glutinosa* suggests that these trees did not grow in Hinterburgsee's catchment and that the high percentages of these pollen types in the sediments are due to long-distance pollen transport. No samples younger than 1300 cal. BP were analysed for macrofossils.

4.5. Chironomids

The samples in the deepest Hinterburgsee sediments (chironomid assemblage zone-1; CAZ-1) are dominated by *Heterotrissocladius grimshawi*-type, *Micropsectra radialis*-type, *Paracladius* and *Procladius* (Fig. 5). At the Younger Dryas/Holo-

cene boundary (ca. 11 500 cal. BP) a single sample shows a very high abundance of *Tanytarsus lugens*-type, whereas *Heterotrissocladius grimshawi*-type and *Paracladius* disappear. *Micropsectra radialis*-type and *Procladius*, however, persist during the whole CAZ-2. In addition, a series of new taxa appear, e.g. *Ablabesmyia*, *Heterotrissocladius marcidus*-type, *Micropsectra* spp., *Microtendipes* and *Stictochironomus*. *Zavrelimyia* A, which is already present in low numbers during the Younger Dryas, shows a first slight increase at the beginning of CAZ-2 only to decrease again during the second part of the zone.

A strong increase of *Zavrelimyia* A and the almost complete disappearance of *Procladius* and *Micropsectra radialis*-type mark the beginning of CAZ-3. The abundance of *Zavrelimyia* A remains high during the rest of the Holocene. CAZ-3 is further characterised by a more or less constant presence of *Chironomus anthracinus*-type and the first occurrences of, among others, *Corynoneura scutellata*-type, *Chironomus plumosus*-type and *Psectrocladius* (*s.str.*). A number of taxa disappear for a short sequence in the middle of the zone around ca. 8600–7600 cal. BP (e.g. *Paratanytarsus* spp., *Cricotopus*-type, *Tanytarsus* A, *Parakiefferiella*; Fig. 5). During the same period *Micropsectra* spp. have their highest abundance. In CAZ-4, *Tanytarsus lugens*-type shows a marked increase and *Procladius* reappears, although the few *Procladius* thoracic horns found in the younger sediments suggest that it is not the same species as in CAZ-1 and 2 (Fig. 5). A number of taxa that were present at the beginning of the zone disappear within CAZ-4, e.g. *Ablabesmyia*, *Heterotrissocladius marcidus*-type and *Micropsectra* spp. Towards the top of the core *Zavrelimyia* A and *Tanytarsus* spp. increase, whereas *Tanytarsus lugens*-type decreases. Total chironomid head capsule concentrations show very large fluctuations in the Hinterburgsee stratigraphy and range from 0.8 to 130 head capsules per cm³ with very low values in CAZ-2 and parts of CAZ-3. Even though the Hinterburgsee stratigraphy is well dated, the calculation of head capsule accumulation rates did not help in the interpretation of the chironomid stratigraphy or explain the large changes in chironomid concentrations.

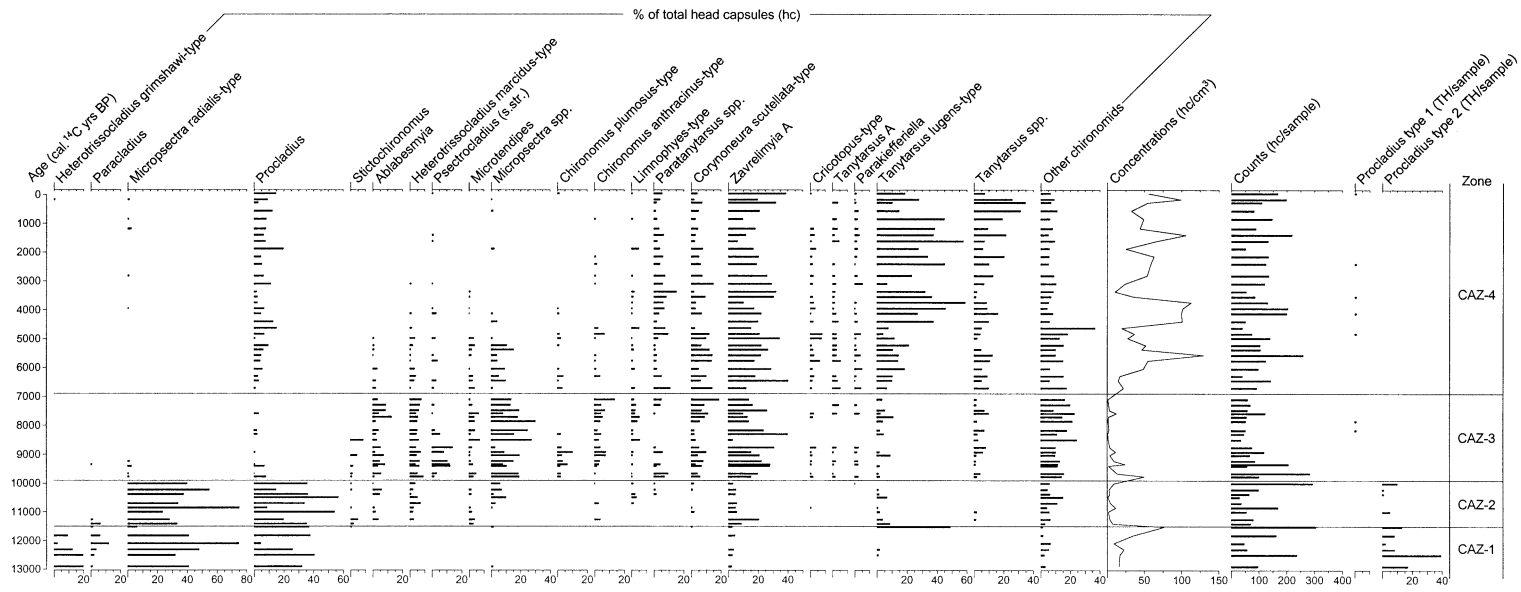


Fig. 5. Chironomid stratigraphy of Hinterburgsee. Larval remains are given as percentages of the total number of head capsules (hc) except for concentrations (hc per cm³) and counts (hc per sample). Pupal remains are given as thoracic horns (TH) per sample.

5. Discussion

5.1. Vegetation development

The Late Glacial and earliest Holocene sediments of Hinterburgsee before 11 000 cal. BP indicate a sparse and treeless vegetation in the lake's catchment (Fig. 4). This agrees with other palaeobotanical studies in the region (e.g. Wegmüller and Lotter, 1990; Tobolski and Ammann, 2000; Wick, 2000), which suggest a treeline in the Bernese Alps below 1300 m asl during the Younger Dryas. At Hinterburgsee local reforestation by *Pinus cembra*, *Betula pubescens* and *Pinus mugo* took place about 500 years after the end of the Younger Dryas (ca. 11 000 cal. BP). *Pinus cembra* and *Betula pubescens* formed the catchment forests for the following 3000 years. However, remains of many pioneer species among dwarf shrubs and herbs, such as *Salix retusa*, *Dryas octopetala*, *Selaginella selaginoides* and *Saxifraga* sp. (Fig. 4), indicate that the vegetation was still fairly open and the soils poorly developed. In addition, the high sedimentation rates and the lithology of the lower part of the core (low organic matter and high carbonate content) suggest high allochthonous sediment input into the lake (Fig. 2b,c). The findings that open *Pinus cembra* and *Betula pubescens* forests formed the woodlands just below the timberline in the Bernese Alps agree well with the results of Wegmüller and Lotter (1990) from two localities ca. 45 km west of Hinterburgsee. According to their study, the subalpine vegetation at timberline in the early Holocene consisted of open stands of *Pinus cembra*, *Betula* and possibly scattered individuals of *Pinus mugo* and *Larix*. However, since strong southerly winds are a common phenomenon in the northern Swiss Alps, the presence of *Larix* pollen at their sites may possibly be the consequence of long-distance transport from the Central Alps. In a palaeobotanical study based on pollen and plant macrofossil analysis of lake sediments, Wick et al. (accepted) studied the Holocene vegetation development near Sägistalsee (1935 m asl), an alpine lake situated 8 km southwest of Hinterburgsee. Their study indicates that *Larix* was never a major constituent of the local vegetation. Our results

support the conclusion of Wick et al. (accepted) that *Larix*, an important component of early Holocene treelines in the Central and Southern Alps, was largely absent from the Hinterburgsee region.

At Hinterburgsee, the first scattered *Abies* macrofossils were found as early as 8200 cal. BP, although it was not until ca. 7400 cal. BP that *Abies* began to expand and became a major component of the local vegetation. This is considerably later than at Sägistalsee, where *Abies* expanded into the lake catchment as early as 8500 cal. BP (Wick et al., accepted). Changes in sediment composition (increase of organic matter and decrease of carbonate) after the expansion of *Abies* (ca. 7100–6000 cal. BP) indicate that the vegetation in Hinterburgsee's catchment became progressively denser and more stable, causing a reduction in allochthonous sediment input into the lake (Fig. 6). As in other lakes in the region (e.g. Wick et al., accepted), *Picea abies* expanded in the catchment of Hinterburgsee at ca. 6000 cal. BP, followed by *Alnus viridis* at ca. 5000 cal. BP. Between 6000 and 5000 cal. BP the concentrations of macrofossils of heliophilous dwarf shrubs and herbs decrease (e.g. *Salix*, *Dryas octopetala*, *Selaginella selaginoides*). Together with the highest organic matter and lowest carbonate content in the sediments, this indicates that the forests were densest in the catchment from ca. 5500 to 2500 cal. BP. During this period *Betula pubescens* declines and *Pinus cembra* and *Abies* all but disappear from the local vegetation at Hinterburgsee.

A first rise in pollen indicating human presence (e.g. *Plantago lanceolata*) is registered in Hinterburgsee as early as 4000 cal. BP. It has been hypothesised that the expansion of *Alnus viridis* in the Alps was promoted by human activity (Wick and Tinner, 1997) and the high abundance of *Alnus viridis* pollen in the Hinterburgsee sediments after ca. 5000 cal. BP may be due to human presence in the region. However, it is not until ca. 2500 cal. BP that clear indications of an opening of the local vegetation are registered in the sediment composition (i.e. a lower concentration of tree macrofossils and a lower organic matter and higher carbonate content of the sediment, suggesting increased erosion). In the last 800 years

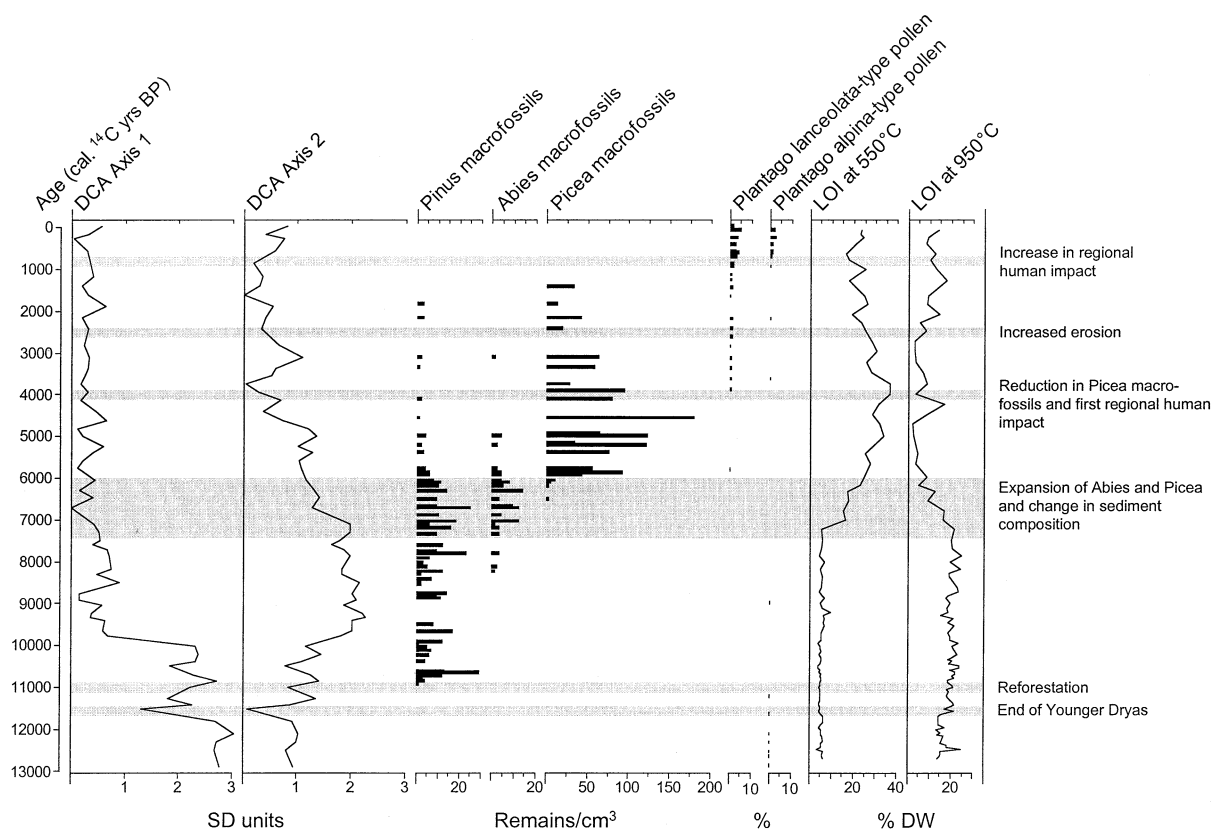


Fig. 6. Catchment events and the development of the chironomid fauna in Hinterburgsee. The chironomid data are summarised in the first two axes of a DCA. Axis scores are given in standard deviation units (SD). LOI, selected pollen types and summary plant macrofossil diagrams for *Pinus*, *Abies* and *Picea* are shown for comparison.

the pollen stratigraphy indicates strong human activity in the region, with a rise in Gramineae and many indicators of pasturing, e.g. *Plantago lanceolata*, *Rumex acetosa* and *Plantago alpina*. Analysed plant macrofossil samples are lacking from the topmost sediments. Nevertheless, the increase in herb pollen to almost 30% indicates that the local vegetation was strongly affected by human activity.

5.2. Major faunistic patterns in the chironomid stratigraphy

Chironomid percentages in the Hinterburgsee sediments show a large amount of high frequency variability downcore, giving the stratigraphy a rather spiky appearance (Fig. 5). This variability seems to be typical of Swiss mountain lakes with

high sedimentation rates (e.g. Heiri, 2001) and is possibly a consequence of the natural variability of the chironomid fauna, of taphonomy, or of the low abundance of chironomid remains in the sediment.

Late Glacial samples in Hinterburgsee (i.e. those before 11 500 cal. BP) show a chironomid assemblage typical of alpine lakes. *Heterotrissocladius grimshawi* and *Micropsectra radialis* have been found in high alpine lakes in Austria (Bretschko, 1974; Zaderer, 1982). In small lakes in Switzerland, *Paracladius* and these two taxa occur mainly above 1750 m asl, whereas *Zavreliomyia* A can be found from 750 to over 2000 m asl (see Heiri, 2001, for distributional data on the chironomid taxa). *Procladius* occurs over a wide temperature gradient in Swiss lakes. However, the pupal remains found in the sediments suggest that

the *Procladius* species present in Hinterburgsee in the Late Glacial and earliest Holocene is a cold stenothermous species. *Procladius* pupal exuviae with similar thoracic horns to *Procladius* type 2 have been described from the High Tatra Mountains, former Czechoslovakia (Gowin and Zavrel, 1944), and have been found in the Central Pyrenees (M. Rieradevall, personal communication) and in Holocene cores from alpine lakes in the French Maritime Alps and the Swiss Alps (O. Heiri, unpublished information).

Heterotrissocladius grimshawi-type and *Paracladius* disappear from the stratigraphy at the end of the Younger Dryas. *Micropsectra radialis*-type and *Procladius* type 2, however, persist well into the Holocene and are joined by a series of new taxa, some with a predominantly alpine/subalpine distribution (e.g. *Micropsectra* spp., *Heterotrissocladius marcidus*-type), others with warmer temperature preferences (e.g. *Ablabesmyia*, *Microtendipes*; see Heiri, 2001). A strong change in the chironomid stratigraphy is apparent at ca. 10 000 cal. BP, with a distinct increase of *Zavrelimyia* A and the almost complete disappearance of *Procladius* and *Micropsectra radialis*-type. From 10 000 cal. BP onwards there is a trend in the stratigraphy from a chironomid assemblage dominated by taxa such as *Micropsectra* spp., *Heterotrissocladius marcidus*-type, and *Ablabesmyia* to one increasingly dominated by *Tanytarsus lugens*-type, with a parallel increase in *Procladius* (presumably *Procladius* type 1) and *Tanytarsus* spp. Other taxa, however, show comparatively little change in the last 10 000 years (e.g. *Coryno-neura scutellata*-type, *Zavrelimyia* A).

Given the clear Holocene succession in both the plant macrofossil and the chironomid stratigraphy, a possible cause for the shifts in the chironomid fauna is changes in the local catchment vegetation. According to our data the following major events can be identified in the catchment development (Fig. 6): (1) the end of the Younger Dryas at ca. 11 500 cal. BP, (2) the reforestation of the catchment by *Pinus cembra* and *Betula pubescens* at ca. 11 000 cal. BP, (3) the expansion of *Abies* between ca. 7400 and 7100 cal. BP with the associated change in sediment composition between ca. 7100 and 6000 cal. BP, (4) the expan-

sion of *Picea* in the catchment at ca. 6000 cal. BP, (5) the reduction of *Picea* macrofossils and the first regional human impact at ca. 4000 cal. BP, (6) the slight change in sediment chemistry at ca. 2500 cal. BP, suggesting an opening of local forests and increased erosion, and (7) the strong increase of grazing indicator pollen at ca. 800 cal. BP, implying a significant increase in local and regional human activity.

For comparison with palaeobotanical and sedimentological data the chironomid results are summarised using DCA (Hill and Gauch, 1980) and plotted on an age scale (Fig. 6). The scaling in 'standard deviation' units of change provides an estimate of species turnover within the chironomid data (Birks, 1998). DCA produced two significant axes (tested following Birks, 1998) that explained 44% of cumulative variance in the chironomid data ($\lambda_1 = 0.65$, $\lambda_2 = 0.25$, total inertia = 2.1). The first axis separates chironomid assemblages before 10 000 cal. BP from younger samples (Fig. 6). On the second axis Late Glacial and early Holocene samples before 10 000 cal. BP have intermediate scores, samples between ca. 10 000 and 7000 cal. BP high scores and between ca. 7000 and 4500 cal. BP there is a gradual trend to the low values that dominate the late Holocene. In a DCA the change in standard deviations per unit of time can provide an estimate of the rate of change within a stratigraphy (e.g. Jacobson and Grimm, 1986). The most abrupt shifts in standard deviation values of the first two axes take place at ca. 10 000 cal. BP and just before and after the Younger Dryas/Holocene boundary (Fig. 6).

At the end of the Younger Dryas, an abrupt increase of temperatures has been inferred for the Alpine region (e.g. Lotter et al., 2000) and this most likely caused the elimination of the alpine taxa *Heterotrissocladius grimshawi*-type and *Paracladius* from Hinterburgsee. A comparison with the plant macrofossil and pollen data reveals that none of the remaining major shifts in the chironomid data coincide with changes in the catchment vegetation (Fig. 6). Just after local reforestation the first DCA axis values show a slight increase. However, this fluctuation is well within the early Holocene variability in DCA axis scores. The changing sediment composition indicates that

the expansion of *Abies* and *Picea* in Hinterburgsee's catchment clearly affected the limnology of the lake (Fig. 6). A gradual decrease in the second axis scores of the chironomid-based DCA begins shortly after the expansion of *Abies*. However, this trend is not very abrupt, not apparent in the first DCA axis, and continues after the expansion of *Picea* in the lake catchment. The organic content of lake sediments has repeatedly been reported as having a significant influence on subfossil chironomid assemblages (e.g. Olander et al., 1999; Laroque et al., 2001). The decreasing trend in DCA axis 2 is accompanied by an increase in sediment organic matter content and a distinct decrease in axis 2 scores takes place synchronously to the initial rise in LOI at 550° at ca. 7000 cal. BP. However, the strongest decrease in this axis takes place later (ca. 4700 cal. BP) when LOI at 550°C is already close to its maximum value. A closer look at the chironomid stratigraphy reveals that this trend is mainly caused by an increase of *Tanytarsus lugens*-type, a taxon with very low second axis scores. In small Swiss lakes, high percentages of *Tanytarsus lugens*-type are restricted to the shallower ones (e.g. all lakes with more than 30% *Tanytarsus lugens*-type head capsules in their surface sediments have a maximum lake depth of 7 m or less; see Heiri, 2001). One of the major complications of using palaeolimnological techniques in lakes with high sedimentation rates over long time scales is that the infilling of the lake basin may change limnological processes (Anderson and Battarbee, 1994) and, therefore, can cause successional trends in aquatic communities. Assuming a constant water surface, the maximum lake depth of Hinterburgsee has decreased from 23 m in the earliest Holocene to 11 m at present. Thus, the successive decrease of lake depth may have been partly responsible for the increasing importance of *Tanytarsus lugens*-type (note, however, that a single early Holocene sample already had a high percentage value of this taxon). The only catchment signal that is clearly paralleled by changes in the chironomid stratigraphy is the rise in pollen, indicating regional pasturing at ca. 800 cal. BP, which is accompanied by an increase in the second DCA axis scores and in *Tanytarsus* spp. (Figs. 5 and 6).

Given the distinct changes in catchment vegetation and sediment composition, the lack of clear corresponding signals in the chironomid stratigraphy is unexpected. Most studies reporting a strong change of aquatic organism assemblages across treeline are from the circumpolar tundra/forest ecotone (e.g. Walker and MacDonald, 1995; Porinchu and Cwynar, 2000; Smol and Cumming, 2000). In these regions the most significant limnological variable changing across treeline (besides temperature) is water chemistry, e.g. pH, the concentrations of nutrients and dissolved organic carbon (DOC; e.g. MacDonald et al., 1993; Pienitz et al., 1999). However, small lakes in the Swiss Alps differ from arctic lowland lakes in a number of important characteristics, such as lake bathymetry, catchment topography and climate. Compared with many continental circumpolar regions the Alps receive a considerable amount of precipitation even in dry regions (Schär et al., 1998) and this, together with the steep topography, leads to high weathering and erosion rates. Lakes with steep catchment slopes seem to be less affected by high DOC concentrations (Rasmussen et al., 1989). Furthermore, as Hinterburgsee is situated on calcareous bedrock it features a high lake water pH and conductivity, and is therefore not prone to acidification. In addition, calcium precipitates humic matter (Stumm and Morgan, 1981, in Rasmussen et al., 1989) and thus DOC may have been rapidly eliminated from the lake.

In modern water chemistry measurements from small Swiss lakes (Müller et al., 1998) there is no clear change across timberline elevation (presently at ca. 1700–1800 m asl in the Northern Alps and up to 2300–2400 m asl in the Central Alps; Burga and Perret, 1998). However, the chemistry of even remote Swiss lakes is influenced by human activity, e.g. by acid precipitation (Boggero et al., 1998) or pasturing and extant lakes may therefore not represent good analogues to assess the relationship between catchment vegetation and lake water chemistry during the early and mid-Holocene. Nevertheless, distributional data on aquatic biota indicate that the strongest changes with altitude presently take place below the timberline in the Swiss Alps (Lotter et al., 1997a).

In the Hinterburgsee stratigraphy the strongest change in the chironomid assemblages clearly occurs at ca. 10 000 cal. BP (Figs. 5 and 6). However, there is no corresponding event in the sedimentological or palaeobotanical data. Furthermore, even though several Holocene climate oscillations have been described for the Swiss Alps and lowland regions (Wick and Tinner, 1997; Haas et al., 1998), none coincides with the disappearance of *Micropsectra radialis*-type and *Procladius* type 2 in Hinterburgsee. According to Kutzbach and Webb (1993), 9000 cal. BP is considered to be the time within the Holocene with the strongest summer insolation in northern temperate and arctic regions and, consequently, to have featured the warmest summer temperatures. Therefore, the disappearance of the last Late Glacial chironomid taxa coincides with a period of slowly but continuously increasing summer insolation. Holocene climate is still poorly understood in the Alpine region and it is not clear if summer temperature followed these insolation changes. However, a gradual increase of early Holocene summer temperature remains a possible reason for the abrupt change of the chironomid assemblages at ca. 10 000 cal. BP. The effects of warmer climate on the cold adapted chironomid fauna could possibly have been aggravated by the decreasing lake depth of Hinterburgsee. Deep lakes often maintain cold (i.e. 4°C) and well oxygenated water in their hypolimnion even in the Swiss lowlands. *Micropsectra radialis*-type head capsules are common in small lakes only at high elevations (Heiri, 2001), but *Micropsectra radialis* is present at low elevations in many of the deep prealpine lakes in northern Switzerland (e.g. Reiss, 1968; Schürch, 1985). As lake depth decreases the susceptibility to anoxia in the profundal increases (Frey, 1988). Furthermore, summer thermal stratification in shallow lakes becomes weaker and this can lead to higher temperatures at the lake bottom (Livingstone and Schanz, 1994). Assuming the same lake level as today, Hinterburgsee's depth has decreased from 23 m at the end of the Younger Dryas to 19 m at 10 000 cal. BP. Possibly the joint pressure of increasing summer temperatures and decreasing lake depth caused the abrupt extinction of the cold adapted Late

Glacial relicts that had previously been able to persevere in Hinterburgsee.

6. Conclusions

In contrast to lakes at the circumpolar treeline, where local reforestation has been shown to rapidly have an effect on aquatic ecosystems (MacDonald et al., 1993; Pienitz et al., 1999), we found no clear relationship between the expansion of forests and the development of the chironomid fauna at Hinterburgsee. The increasingly dense woodlands in the catchment may have influenced the chironomid fauna by reducing erosion and increasing the organic matter content of the sediments. However, the succession in the chironomid stratigraphy between ca. 7000 and 4000 cal. BP (Fig. 6) may also have been caused or reinforced by the sediment infilling of the lake basin. Our results suggest that the effect of changing catchment vegetation on the chironomid fauna may be less pronounced in subalpine lakes than in subarctic lowland lakes. However, Hinterburgsee is only a single-case study. As the lake is situated on calcareous bedrock with high erosion rates it is not susceptible to acidification or to high DOC concentrations, factors which affect the limnology of lakes at the arctic treeline. Subalpine lakes on silicate bedrock or with more gentle catchment slopes may react differently to catchment reforestation and tree immigration. Finally, most inferences of lake water chemistry changes due to catchment reforestation are based on algal microfossils (Lotter et al., 1999; Smol and Cumming, 2000). Due to the high content of clay and silt in parts of the sediments, diatom analysis was not possible for Hinterburgsee. The inclusion of diatoms in future studies addressing the effect of catchment vegetation on subalpine lakes would provide important supplementary information on water chemistry changes too weak to be registered by the chironomid fauna.

None of the major Holocene events in Hinterburgsee's catchment caused a clear and immediate reaction in the chironomid fauna, with the possible exception of the increased human impact during the last ca. 800 years. For subalpine lakes on

calcareous bedrock in the Alps this implies that reforestation and tree immigration are not likely to cause a distinct short-term bias in chironomid-based climate reconstruction. However, the long-term development of soils and forests may possibly be responsible for trends on a longer time scale in chironomid stratigraphies. Therefore, chironomid-inferred Holocene climate reconstructions in the Alpine region should ideally be based on a number of sites with a different vegetation and catchment history (e.g. different forest types or different immigration ages for dominant tree species) to reduce the possibility of an error in the reconstruction due to catchment–lake interactions. The quantity and preservation of tree macrofossils may differ substantially from one tree species to the next (e.g. Ammann and Wick, 1993) and the density of catchment forests may be difficult to assess based on plant macrofossil analysis alone. Sediment composition and changes in sedimentation rates provide useful supplementary information to assess the effects of catchment vegetation changes on sedimentological processes in the lake. Chironomid-inferred climate signals that parallel distinct changes in sediment composition should certainly be treated with caution.

Although this study suggests that catchment vegetation changes are not a major factor affecting the Holocene development of chironomid assemblages in subalpine lakes in the Alpine region, further work is needed to resolve the issue. An important question that remains to be answered is whether the influence of vegetation on the chironomid fauna is more distinct in subalpine lakes with smaller catchments and gentler catchment topography, or in lakes on silicate bedrock.

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