

Zeitschrift: Eclogae Geologicae Helvetiae
Herausgeber: Schweizerische Geologische Gesellschaft
Band: 93 (2000)
Heft: 3

Artikel: A Holocene fossil coleopteran (beetle) assemblage from the Central Swiss Alps : climate and ecology
Autor: Jost-Stauffer, Monika
DOI: <https://doi.org/10.5169/seals-168835>

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A Holocene fossil coleopteran (beetle) assemblage from the Central Swiss Alps: Climate and ecology

MONIKA JOST-STAUFFER

Key words: Fossil beetles, fen peat, palaeoenvironment, timberline, Central Swiss Alps, Holocene

ABSTRACT

The beetle fauna of a fen peat melted out in pieces from below the retreating Unteraar Glacier was examined. The sediment (12 kg of peat) yielded more than 5000 insect fragments. Identification of the fossils provided a detailed picture about palaeoenvironment in the Gletschervorfeld 3600–3800 yr BP ago. Coleopterans living in marshy alpine areas near lakes and running water associated with reeds and moss dominate the assemblage. Species indicating persisting snow patches even during summer months are *Helophorus glacialis* and *Nebria castanea*. Many of the specimens reported live in flowering meadows and shrubs (often *Rhododendron*, *Alnus*, *Salix*). There are several species in the assemblage which are not known to live in the alpine zone (e.g. *Stenus bifoveolatus*, *Gymnusa brevicollis*). These observations and the total absence of tree-dependent species suggest that the ancient Cyperaceae fen peat was growing in the subalpine dwarf-shrub heath - above the forest limit but below the treeline. From the finding of wood fragments in the same deposits, the presence of isolated trees can be inferred, probably on the slopes where the conditions were locally more favourable. Reconstructed July temperatures based on the beetle assemblage yielded a mean value similar to today's temperature measured 5.5 km east from the site at Grimsel Hospiz.

ZUSAMMENFASSUNG

Im Zusammenhang mit dem aktuellen Gletscherrückzug wurde die Käferfauna eines Flachmoors untersucht, das in Stücken aus dem Unteraargletscher geschmolzen wurde. Die Untersuchung von 12 kg Torf lieferte mehr als 5000 Insektenreste. Anhand der Fossilien war es möglich, ein detailliertes Bild der Umgebung des Gletschervorfeldes vor 3600–3800 yr BP zu erhalten. Die Fauna wird dominiert von Arten, die sumpfiges Habitat bevorzugen, in der Nähe von Seen und fliessenden Gewässern leben und mit Seggen und Moos assoziiert sind. Zwei Spezies (*Helophorus glacialis* und *Nebria castanea*) weisen auf die Anwesenheit von Schneeflecken, auch während der Sommermonate, hin. Viele der bestimmten Arten leben auf blühenden Wiesen und Büschen (bevorzugt *Rhododendron*, *Alnus* und *Salix*). Es gibt mehrere nicht-alpine Arten in der Faunenvergesellschaftung (z.B. *Stenus bifoveolatus*, *Gymnusa brevicollis*). Diese Beobachtungen sowie die vollständige Abwesenheit von Coleopterenarten, die von Bäumen abhängig sind, führen zum Schluss, dass das Cyperaceen-Flachmoor zur Zeit seiner Entstehung in der subalpinen Zwergstrauchstufe lag – oberhalb der Wald-, aber unterhalb der Baumgrenze. Einzelne Holzfragmente in den torfigen Ablagerungen lassen auf die Existenz einzelner Bäume in der Nähe schliessen. Wahrscheinlich wuchsen diese an den Hängen, ähnlich der heutigen Situation, wo das Klima lokal vorteilhafter ist. Die Käferfauna wurde zur Rekonstruktion einer mittleren Julitemperatur verwendet. Sie ergab einen ähnlichen Wert dem heutigen, wie er 5.5 km weiter östlich am Talausgang beim Grimsel Hospiz gemessen wird.

Introduction

In the summer of 1995, tree stems and pieces of a Cyperaceae fen peat were found in the Vorfeld of the Unteraar Glacier (Central Alps of Switzerland) (Fig.1). Due to the actual retreat, they were eroded from the glacier's bed, transported by meltwater outburst and deposited just in front of the glacier at an altitude of 1920 m a.s.l. It could be seen with the naked eye that the cake-shaped organic sediment clasts were full of insect fragments.

The analysis of coleopteran assemblages to reconstruct palaeoclimate and palaeoenvironments is well established (Atkinson et al. 1986, 1987; Coope et al. 1998). In the region of the Alps, only a few investigations about fossil beetles have been made so far. Ponel (1992, in: Tessier et al. 1993) used the

method to reconstruct timberline fluctuations in the French Alps. A study of a high altitude site in the Pyrénées has recently been carried out by the same author (Ponel et al. 1999).

During the last decades, different records have been included to register Holocene climatic oscillations in the Alps. Gamper & Suter (1982) made a compilation of data from different authors. "25 000 Jahre Gletschergeschichte" is the title of a publication where Furrer (1990) summarised twenty years of research of Swiss glaciers at the University in Zurich. Several articles about treeline fluctuations in the Swiss Alps during the Holocene are included in "Oscillations of the Alpine and Polar Tree Limits in the Holocene" (Frenzel, ed. 1993). Beside dendrochronology, glacial morphology, fossil soils, pollen

Geologisches Institut Universität Bern, Baltzerstrasse 1, CH-3012 Bern, Switzerland

and plant macrofossils, insect analysis is able to furnish important data to complete the picture about Holocene palaeoenvironment.

Locality and History

The Unteraar Glacier is situated north of the Grimsel Pass in the Bernese Oberland. It is the fourth largest ice-stream of the Alps. Zumbühl (in: Zumbühl & Holzhauser 1988) describes the Unteraar Glacier as the cradle of glacial field research: the first cartographic depiction dates back to the beginning of the eighteenth century. Famous naturalists like Scheuchzer, Escher, Agassiz and others visited and described the impressive glacier, which is 6 km long today. Since 1876, the Unteraar Glacier has been retreating at an average of 16.9 m per year (²Data from World Glacier Monitoring Service). Investigations did not stop in this century. Frey (1921, 1922) made detailed descriptions about the vegetation before inundation. In 1931 the Vorfeld Aarboden was dammed to gain hydroelectric power. Glaciological studies were carried out by Haefeli (1970), Gudmunsson (1994) and others. The area of the Grimsel Pass attracted entomologists too (C. Huber, personal communication 1999). As far as the author knows, however, there is no literature which deals specifically with the Unteraar region. The finds made by different collectors were recorded in general overviews of distribution of beetle species in Switzerland (e.g. Marggi 1992, Puthz 1981, Comellini 1974).

Radiocarbon dating

To date the peat, six radiocarbon measurements were carried out by Hormes et al. (1998). Five twigs of *Salix* sp. extracted from the peat and one bulk sample were dated. The measurements were made at the underground laboratory of Climate and Environmental Physics at the University of Bern using the conventional β -counting method. The samples yielded ages between 3789 ± 25 and 3622 ± 31 conventional radiocarbon years before present. According to the small range of ¹⁴C-dated samples, we conclude that they belong to the same fen peat unit.

Material and Methods

Thirteen peat samples of 1 kg to 5 kg were processed. They were sawed into two halves. One half was used for insect analysis, the second half put aside for ¹⁴C and other investigations. The compressed and hard peat was composed of sedges, brown moss, flattened twigs and silty layers. Twelve kilograms of sediment yielded more than 5000 insect fragments.

To extract the insects, the standard process described by Coope (1986) and Elias (1994) was applied. In a first step, the sediment was put in a plastic bowl and soaked in water, then gently split by hand along the layers. Due to its solid consistency, the material had to be soaked in a weak sodium carbonate (Na_2CO_3) solution for several days and heated at low temperature for a few hours. The sediment was dispersed again by hand. To remove mineral particles such as silt and fine sand, the slurry was washed several times through a sieve of 300 micron mesh diameter. Once the detritus had been screened, a handful of the residue was placed in a bowl and thoroughly mixed with paraffin. This treatment makes the smooth impermeable insect sclerites adhere to the oil. When cold water is added to the mixture, the oil and insects float on the surface. The floating fraction was carefully decanted. This process had to be repeated until no insect remains were floating on the surface anymore. To remove the paraffin, the concentrate was first washed with detergent and then with ethanol. Since some plant debris was inevitable decanted together with the insect remains, the decanted fraction had to be sorted under a binocular microscope. Heavily sclerotised fragments of Coleopterans were mounted on cards used in micropalaeontology with a water-soluble glue. Frail and small elements were put in vials and stored in ethanol.

Insect analysis

Identification of fossil insects requires a modern reference collection. Keys of present-day Coleoptera are based on exoskeletal criteria and therefore useful to distinguish fossil species. However, as they are always based on whole specimens, they are helpful only to certain extent. An exception is Goecke (1943) who provides a key to the elytra of European Donaciinae (leaf beetles). In general, we worked with the series of Freude et al. (1964–83) and the supplementary volumes of Lohse & Lucht (1992). The illustrations in Reitter (1908–16) were useful in cases where the assignment to a family was difficult. Special literature was needed for *Helophorus* sp. (Angus 1992), the Omaliines (Zanetti 1987), *Olophrum* sp. (Campbell 1983) and *Aphodius* sp. (Dellacasa 1983). In many cases, direct comparison with modern material combined with taxonomic instruction led to successful identification.

However there are groups of beetles that cannot be identified to species level if only preserved in fragments. One example is the subfamily Aleocharinae. Individuals that could not be unambiguously assigned to a species (indicated by “cf.”) were not included in ecological and climatic interpretation of the fauna. Specimens identified by the author were checked by different specialists.

In some cases, male genitalia found in the sediment could be assigned to a genus. The aedeagus (male genitalia) is diagnostic for many coleopteran species and the most certain criterion for identification. Several abdomens of the staphilinid beetle *Stenus bifoveolatus* were preserved together with the

² World Glacier Monitoring Service, Swiss Federal Institute of Technology, Laboratory of Hydraulics, Hydrology, and Glaciology, Gloriastrasse 37/39, CH-8092 Zurich, Switzerland

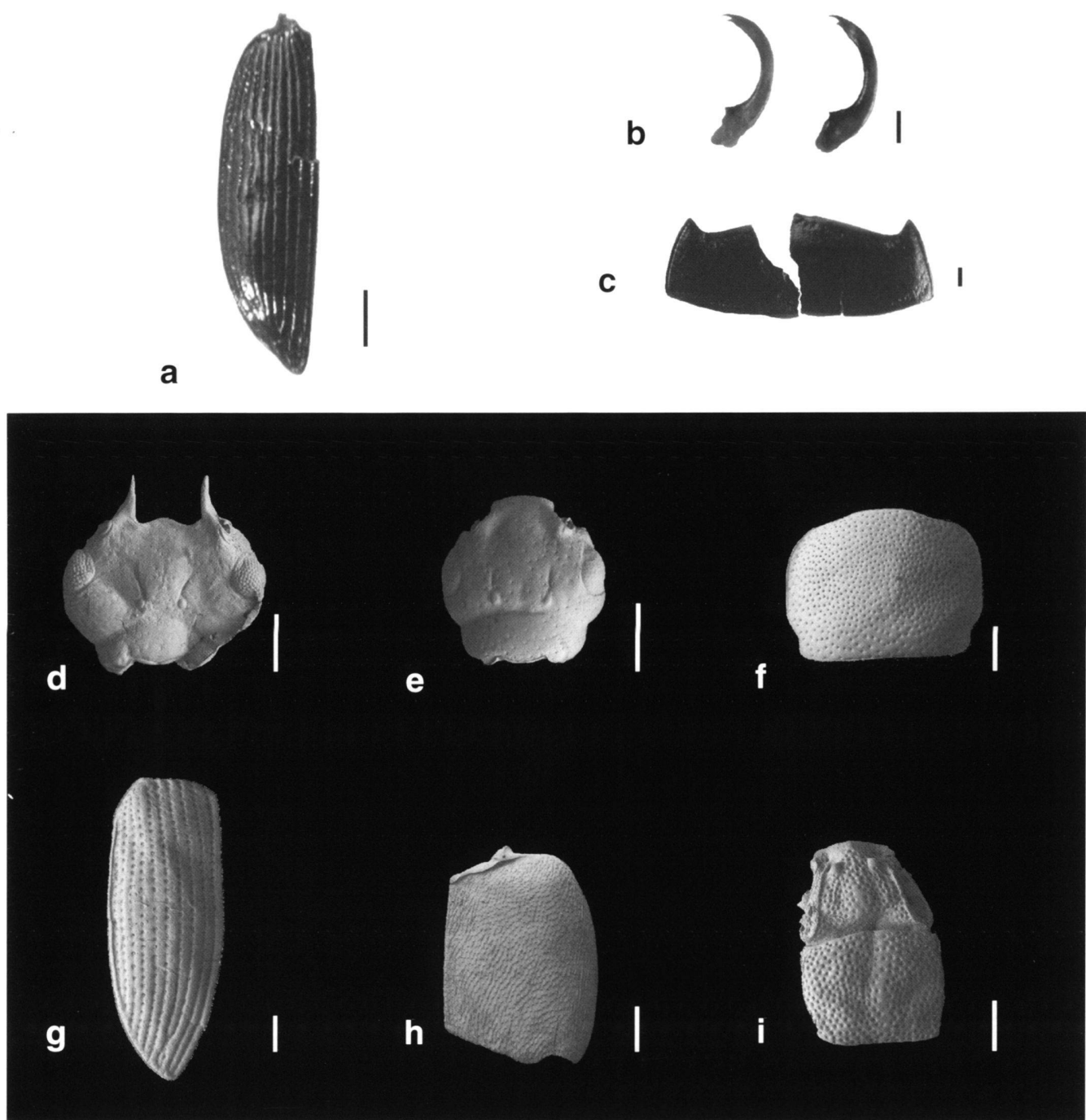


Plate 1.
Fragments of fossil Coleoptera photographed with different techniques

The scale bar is 1 mm in a, and 0.25 mm in b–i

Fig. a photographed with digital camera
left elytron of *Nebria castanea* Bon.

Fig. b and c conventional photographs on microscope
b modern (left) and fossil (right) aedeagus of *Agabus congener* (Thunb.)
c pronotum of *Agabus congener* (Thunb.)

Figs. d–i scanning electron micrographs
d head of male *Anthophagus alpinus* (F.)
e head of *Eucnecosum brachypterum* (Grav.) / *tenue* (LeConte)
f pronotum of *Olophrum consimile* (Gyll.)
g left elytron of *Helophorus glacialis* Villa
h right elytron of *Gymnusa brevicollis* (Payk.)
i head and pronotum of *Stenus bifoveolatus* Gyll.

aedeagus. After the provisional identification of a pronotum as *Agabus congener* (Dytiscidae) (Plate 1, Fig. c), we recognised an isolated male genitalia of this species in the same sample (Plate 1, Fig. b), which confirmed the identification.

Faunal assemblage

The most abundant sclerites found in the peat are derived from beetles. Remains from spiders, ants, caddisflies, mites, Chalcidoidea, Tipulidae and Diptera were picked out and stored but not yet further identified. In the discussion of the beetle assemblage, the fossil content of the thirteen samples will be considered as a single unit since they are very similar to one another and the radiocarbon dates suggest that they all belong to the same fen peat unit.

For each species in the faunal list (Table 1), the minimum number of individuals is calculated from the maximum number of any identifiable skeletal element. An example: Four left elytra, two right elytra, three pronota and one head of a certain species gives a minimum number of four individuals.

The abundance of staphilinids (rove beetles) in species and number of individuals is remarkable. *Eucnecusum brachypterum/tenuis*, *Olophrum consimile* and *Stenus bifoveolatus* (Plate 1, Fig. e, f, i) are represented by hundreds of fragments. All three species are hygrophilous and require a similar habitat. It has to be mentioned that *Stenus bifoveolatus* and *Gymnusa brevicollis* (Plate 1, Fig. h) are not occurring in the alpine zone (Koch 1989).

<i>Olophrum consimile</i> (Gyll.) formerly <i>Olophrum alpinum</i> (Heer)	associated with Cyperaceae, Graminae and moss along running water in alpine habitats (pers. comm. Zanetti 1999)
<i>Eucnecusum tenue</i> (LeConte)	associated with Cyperaceae in alpine lakes and marshes (pers. comm. Zanetti 1999)
<i>Stenus bifoveolatus</i> Gyll.	typical marsh inhabitant, occurring from the plain up to 1800 m a.s.l. (pers. comm. Puthz 1998)
<i>Gymnusa brevicollis</i> (Payk.)	mires, marshy surroundings, typhophilous, often in <i>Sphagnum</i> , not alpine (Koch 1989)

Aquatic species such as the dytiscid beetles *Agabus congener*, *Hydroporus memnonius* and *Hydroporus nigrita* are found in marshy waters. Focarile (1981) reports *H. memnonius* as typical for small lakes with vegetation at altitudes of 1900–2000 m in Kanton Tessin.

<i>Hydroporus nigrita</i> (F.)	cold-stenothermal, acidophilous, shady springs, fen pools and mountain streams, forest streams rich with leaves (Koch 1989)
<i>Hydroporus memnonius</i> Nic.	stenotopic, acidophilous, marshy waters, pools in wood rich with leaves (Koch 1989)
<i>Agabus congener</i> (Thunb.)	stenotopic, marshy waters (Koch, 1989). Recorded as high as 2200 m a.s.l. (Freude, Harde & Lohse 1971)

There are several cold-stenothermal species belonging to different families. Among the Carabidae (ground beetles) there is *Nebria castanea* (Plate 1, Fig. a), a wingless species, which is often found near melting snow. The dung beetle *Aphodius abdominalis* is mainly reported from the dwarf-shrub heath and along snowfields. Focarile (1985) mentions the staphilinid *Quedius punctatellus* as a species living in alpine meadows and accidentally occurring in the *Alnetum*. According to Koch (1989) it is also found in snow depressions. Horion (1965) reports that it is frequently occurring in subalpine forests. Among the cold tolerant taxa the water beetle *Helophorus glacialis* (Plate 1, Fig. g) needs the most severe climatic conditions. It lives on the edges of snow patches and in meltwater ponds. The presence of this hydrophilid "suggests the persistence of snow-patches in summer" (Ponel 1997).

<i>Nebria castanea</i> Bon.	everywhere in mountain areas, damp and wet sites, mostly close to melting snow (Marggi 1992)
<i>Helophorus glacialis</i> Villa	"a northern and mountain species ... It is typically found in areas just uncovered by melting snow" (Angus 1992)
<i>Quedius punctatellus</i> Heer	numerous in moss, at high altitudes (Comellini 1997). Forests, zone of larch and green alder, alpine meadows, snow depressions (Koch 1989)
<i>Aphodius abdominalis</i> (Bon.)	mainly in the dwarf-shrub heath, also in <i>Loiseleurietum</i> and on the edges of snow patches (Koch 1989)

Beside the already mentioned species living in moss and reeds, the surrounding vegetation is indicated by some Omaliines, a subfamily of staphilinids. They indicate flowering meadows and brushwood (Zanetti 1987). The aquatic leaf beetles *Donaia* and *Plateumaris* feed on different sedges. As its name implies, the small weevil (Curculinidae) called *Rhynchaenus salicis* depends on the willow (*Salix* sp.).

<i>Eusphalerum alpinum</i> (Heer)	flowering meadows in subalpine and alpine regions (Zanetti 1987)
<i>Amphichroum hirtellum</i> (Heer)	flowering shrubs, especially <i>Alnus</i> and <i>Rhododendron</i> (Zanetti 1987)
<i>Anthophagus bicornis</i> (Block)	on shrubs, mountainous and subalpine regions (Zanetti 1987)
<i>Anthophagus alpinus</i> (F.)	on shrubs, especially <i>Rhododendron</i> , subalpine regions (Zanetti 1987)
<i>Anthophagus omalinus</i> (Zett.)	on shrubs, mountainous and subalpine regions (Zanetti 1987)
<i>Plateumaris sericea</i> (L.)	oligophagous on <i>Carex</i> sp. (Koch 1992)
<i>Rhynchaenus salicis</i> (L.)	oligophagous on <i>Salix</i> sp. (Koch 1992)

Before drawing any conclusions about paleoecology, we have to ask whether the fauna in this present case is autochthonous (Ponel & Richoux 1997). Many beetles are good fliers or can be transported by wind. Further, streams could have brought in some of the insects. Ponel (1997) examined a high altitude site in the Northern Apennines and reported an influx of wind-blown elements. Kenward (1975, 1976) investigated death assemblages from a drain and from roof gullies. He emphasises

that the background fauna (i. e. the transported component) may be predominant where the local fauna is sparse. For Kenward, reliable evidence that fossils lived close to the point of deposition is the abundance of a group of species with similar requirements, as long as the total fauna is large. If a certain species is represented by numerous individuals, it could be an indication that it was attracted to the site of the deposit or its surroundings or maybe even that it did breed there. These conditions recommended for the reconstruction of past environments at the Unteraar site are fulfilled: The fauna is large, some species are represented by a large number of individuals. The fossil assemblage contains many species of different families with very similar ecological requirements. Even very frail sclerites are in a good state of preservation, which indicates that they have not been transported over long distances after death. Fossils of insects and their host plants when found together in the same samples confirm that the assemblage is largely in situ.

The ecology depicted by the beetle fauna is very consistent in itself. An overwhelming abundance of hygrophilous Coleoptera suggests a marshy habitat with a pond but also running water nearby. Species exclusively dependent on trees are absent. There are some species in the assemblage though that are not known to occur in alpine areas. The information furnished by different specimens about the vegetation indicates a position in the dwarf-shrub heath. We locate the ancient fen peat in the upper subalpine zone, above the forest limit but below treeline.

Climatic reconstruction

Quantitative estimates of paleotemperatures based on coleopteran assemblages can be made by using the Mutual Climatic Range method (MCR). This method, developed by Atkinson et al. (1986) uses the correlation between the modern distribution of a particular beetle species and thermal climatic factors, which are measured by meteorological stations. Each species can be plotted on a climatic envelope defined by T_{\max} (the mean temperature of the warmest month) and T_{range} (the difference between the mean temperature of the warmest month and the mean temperature of the coldest month). T_{\min} (the mean temperature of the coldest month) can be calculated from these two co-ordinates. The area of overlap of the climatic envelopes of the species comprising the fossil community is called the mutual climatic range and defines the paleoclimatic conditions. Tests of this method on modern beetle faunas showed slight systematic deviations which can be avoided using correction equations (Atkinson et al. 1987). In the following case we applied the slightly revised version of the regression equations as published in Coope et al. (1998).

To reconstruct T_{\max} and T_{\min} from the Unteraar fen peat, twelve species with established climatic envelopes were used:

Nebria rufescens
Pterostichus diligens/strenuus

Hydroporus memnonius
Agabus congener
Helophorus glacialis
Omalium excavatum
Eucnecosum brachypterum/tenu
Acidota crenata
Anthophagus bicornis
Tachinus elongatus
Gymnusa brevicollis
Aegialia sabuleti

Calculation of temperature for this assemblage provided the following results:

Unteraar, 1920 m a.s.l., 3789 \pm 25 to 3622 \pm 31 yr BP (^{14}C age)
 T_{\max} median (calibrated) = 9.0°C
 T_{\min} median (calibrated) = -7.7°C

These temperatures may be compared with the actual ones, measured at the Grimsel Hospiz, 5.5 km east of the Unteraar site (Fig. 1):

Grimsel Hospiz, 1950 m a.s.l., 1964–1998
 average temperature of July = 9.5°C
 average temperature of January = -5.3°C

It is conspicuous how similar T_{\max} , inferred from the fossil beetle assemblage, is to the average of the measured July temperatures of the last 35 years at Grimsel Hospiz. According to these values it was slightly cooler during the warmest month (0.5°C) between 3800 and 3600 yr BP than today. But this small difference is probably within the experimental limits of the MCR method. The value calculated by the MCR method for the coldest month (T_{\min}) suggests a temperature in January that was about 2.5°C lower.

Comparing temperatures from Unteraar and the Hospiz however we have to bear in mind that in spite of the short distance microclimate can be different. Frey (1921, p.107) reports that temperatures measured in summer 1918 at the bottom of the valley near the glacier were 2° C higher than further along the valley. Further on it is likely that the water sheet of the dammed Unteraar Lake influences (buffers) the temperatures at Grimsel Hospiz today.

Discussion and Conclusions

During the growth of the fen peat, the Unteraar Glacier was smaller than today. The fossil beetle assemblage contains no tree-dependent species suggesting that trees may not have been growing in the immediate vicinity of the peat at that time. Among the dated wood fragments however (Hormes et al. 1998), there were three samples within the range of peat growth. One sample was *Pinus cembra*, another *Picea* sp. and a third either *Picea* or *Larix*. In the peat we found a male in-

Table 1. List of Coleoptera arranged in the systematic order proposed by Freude, Harde and Lohse (1965–83). The numbers indicate the minimum number of individuals per sample.

Species	Sample number													Total number of individuals
	1	2	3	4	5	6	7	8	9	10	11	12	13	
CARABIDAE														
<i>Cicindela hybrida transversalis</i> Dej.	1	-	-	-	-	-	-	-	-	-	-	-	-	1
<i>Nebria rufescens</i> Ström	1	-	-	-	-	-	-	-	-	-	-	-	-	1
<i>Nebria castanea</i> Bon.	-	-	1	-	-	-	-	-	-	1	-	-	1	3
<i>Pterostichus strenuus</i> (Panz.) / <i>diligens</i> (Sturm)	-	-	-	-	-	-	-	-	-	-	1	-	-	1
DYTISCIDAE														
<i>Hydroporus nigrita</i> (F.)	-	2	2	-	-	-	-	1	-	8	1	1	-	15
<i>Hydroporus memnonius</i> Nic.	1	-	9	-	-	-	-	-	-	-	2	-	-	12
<i>Hydroporus</i> spp.	1	-	5	1	-	4	-	1	-	7	3	-	-	22
<i>Agabus biguttatus</i> (Ol.)	1	-	-	-	-	-	-	-	-	-	-	-	-	1
<i>Agabus congener</i> (Thunb.)	-	-	1	-	-	-	-	-	-	1	-	1	-	3
<i>Agabus</i> cf. <i>congener</i>	-	-	-	-	-	-	-	-	-	-	-	-	1	1
<i>Agabus</i> sp.	-	1	-	-	-	-	-	-	-	-	-	-	-	1
HYDROPHILIDAE														
<i>Helophorus glacialis</i> Villa	-	1	-	1	-	4	-	1	1	19	3	-	1	31
<i>Enochrus ochropterus</i> (Marsh.)	-	-	-	-	-	-	-	-	-	1	-	-	-	1
<i>Enochrus ochropterus</i> (Marsh.) / <i>quadripunctatus</i> (Hrbst)	-	-	-	-	-	-	-	-	-	1	-	-	-	1
STAPHILINIDAE														
cf. <i>Proteinus</i>	-	-	-	-	-	-	-	1	-	-	-	-	-	1
<i>Eusphalerum alpinum</i> (Heer)	2	-	1	-	-	-	-	-	1	3	2	-	-	9
<i>Eusphalerum</i> cf. <i>alpinum</i>	-	-	-	-	-	-	-	-	-	2	-	-	-	2
<i>Eusphalerum anale</i> (Er.)	-	-	-	-	-	1	-	-	-	-	-	-	-	1
<i>Eusphalerum</i> cf. <i>limbatum</i> (Er.)	-	-	-	-	-	-	-	-	-	1	-	-	-	1
<i>Eusphalerum</i> spp.	2	2	-	-	1	-	2	-	2	6	2	1	-	18
<i>Omalium caesum</i> Grav.	-	1	-	-	-	-	-	-	-	-	-	-	-	1
<i>Omalium excavatum</i> Steph.	-	-	-	-	-	-	-	-	-	-	-	1	-	1
<i>Omalium</i> sp.	-	-	1	-	1	1	-	1	-	-	-	-	2	6
<i>Olophrum consimile</i> (Gyll.), jun. syn. <i>O. alpinum</i> (Heer)	16	12	9	10	7	5	7	6	3	51	24	5	20	175
<i>Olophrum</i> sp.	31	2	2	11	2	2	-	6	1	1	12	1	23	94
<i>Eucnecosum brachypterum</i> (Grav.) / <i>tenu</i> (LeConte)	68	122	13	53	23	10	8	26	8	117	95	122	59	724
<i>Acidota crenata</i> (F.)	-	-	-	-	-	-	-	-	1	-	-	-	-	1
<i>Amphichroum canaliculatum</i> (Er.) / <i>hirtellum</i> (Heer)	1	6	-	1	6	-	1	1	3	1	-	-	-	20
<i>Amphichroum hirtellum</i> (Heer)	6	2	-	4	1	11	-	-	-	30	11	1	5	71
<i>Lesteva</i> cf. <i>monticola</i> Kiesw.	-	-	-	-	-	-	-	-	-	1	-	-	-	1
<i>Anthophagus bicornis</i> (Block)	-	-	-	-	-	1	-	-	-	-	1	-	-	2
<i>Anthophagus</i> cf. <i>bicornis</i>	1	-	2	-	-	-	-	-	-	1	-	-	-	4
<i>Anthophagus alpinus</i> (F.)	5	1	-	-	2	5	-	-	-	9	4	-	-	26

<i>Anthophagus alpinus</i> (F.) / <i>fallax</i> Kiesw.	6	3	1	1	-	-	-	2	-	11	2	-	3	29
<i>Anthophagus omalinus</i> Zett.	4	2	1	2	-	3	-	2	-	7	4	-	1	26
<i>Anthophagus</i> cf. <i>omalinus</i>	-	-	-	-	-	-	-	-	-	1	-	-	-	1
<i>Anthophagus</i> cf. <i>alpestris</i> Heer	-	-	-	-	-	-	-	-	-	-	-	-	1	1
<i>Anthophagus</i> spp.	-	3	1	1	1	6	5	3	2	13	3	2	1	41
<i>Stenus</i> cf. <i>gallicus</i> Fauv.	-	-	1	-	-	-	-	-	1	-	-	1	1	4
<i>Stenus</i> cf. <i>pusillus</i> Steph.	-	-	-	1	-	-	-	-	-	-	-	-	-	1
<i>Stenus</i> cf. <i>oscillator</i> Rye	-	-	-	-	-	-	-	-	1	-	-	-	-	1
<i>Stenus bifoveolatus</i> Gyll.	45	19	13	14	27	3	7	2	4	8	21	65	10	238
<i>Stenus</i> sp.	-	2	-	-	-	-	-	2	-	-	1	2	-	7
<i>Philonthus</i> spp.	-	2	-	-	-	-	-	-	-	1	1	-	1	5
<i>Gabrius</i> spp.	-	2	-	-	-	-	-	-	-	-	1	-	-	3
<i>Quediini</i> indet	-	-	-	-	-	1	-	-	-	-	-	-	1	2
<i>Quedius punctatellus</i> Heer	1	1	1	1	1	-	-	1	1	1	-	-	1	9
<i>Quedius</i> spp.	-	-	1	1	-	1	-	-	1	-	-	-	-	4
<i>Mycetoporus</i> s.l.	-	-	1	-	-	-	-	-	-	-	-	-	-	1
<i>Tachinus elongatus</i> Gyll.	-	-	-	-	-	-	-	-	-	1	-	-	-	1
Aleocharinae indet	9	28	10	8	4	2	-	2	2	19	14	18	5	121
<i>Gymnusa brevicollis</i> (Payk.)	1	1	5	1	1	-	-	-	-	1	4	2	-	16

SCARABAEIDAE

<i>Aegialia sabuleti</i> (Panz.)	-	1	-	-	-	-	-	-	-	-	-	-	-	1
cf. <i>Aegialia sabuleti</i>	1	-	-	-	-	-	-	-	-	-	-	-	-	1
<i>Aphodius abdominalis</i> (Bon.)	1	1	-	1	1	-	-	1	-	1	1	-	-	7

SCIRTIDAE

<i>Cyphon</i> sp.	-	-	-	-	-	-	-	-	-	4	-	-	-	4
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BYRRHIDAE

<i>Cytilus sericeus</i> (Forst.)	1	-	-	-	-	-	-	-	-	-	-	-	-	1
<i>Cytilus sericeus</i> (Forst.) / <i>auricomus</i> (Duft.)	-	-	2	-	-	-	-	-	-	-	-	-	-	2
<i>Byrrhus</i> sp.	-	-	-	-	-	1	-	-	-	1	-	-	-	2

CHRYSOMELIDAE

<i>Donacia impressa</i> Payk.	-	-	-	-	-	-	-	-	-	1	-	-	-	1
<i>Donacia impressa</i> Payk. / <i>aquatica</i> (L.)	-	-	-	-	-	-	-	-	-	1	-	-	-	1
<i>Donacia</i> cf. <i>brevitarsis</i> Thoms.	-	-	-	-	-	-	-	-	-	1	-	-	-	1
<i>Donacia obscura</i> Gyll.	-	-	1	-	-	-	-	-	-	-	-	-	-	1
<i>Donacia</i> cf. <i>obscura</i>	1	-	-	1	-	-	-	-	-	-	-	-	-	2
<i>Donacia</i> cf. <i>thalassina</i> Germ.	-	-	-	-	-	-	-	-	-	1	-	-	-	1
<i>Donacia vulgaris</i> Zsch.	-	-	-	-	-	-	-	-	-	1	-	-	-	1
<i>Donacia</i> spp.	-	1	-	1	1	1	-	-	-	-	1	-	-	5
<i>Plateumaris sericea</i> (L.)	1	-	1	-	1	-	-	-	-	1	-	-	-	4
<i>Phratora</i> sp.	-	-	-	-	-	-	1	-	-	-	-	1	1	3
<i>Altica</i> cf. <i>lythri</i> Aubé	-	-	-	-	-	-	-	-	-	-	2	-	-	2
<i>Altica</i> sp.	-	-	-	-	-	-	-	-	-	-	-	2	-	2

CURCULIONIDAE

Curculinidae indet	1	1	-	-	1	-	-	1	-	1	-	-	-	5
<i>Rhynchaenus salicis</i> (L.)	-	-	-	1	-	-	-	-	-	1	-	-	-	2
<i>Rhynchaenus</i> sp.	-	-	-	1	-	-	-	-	-	-	1	-	-	2

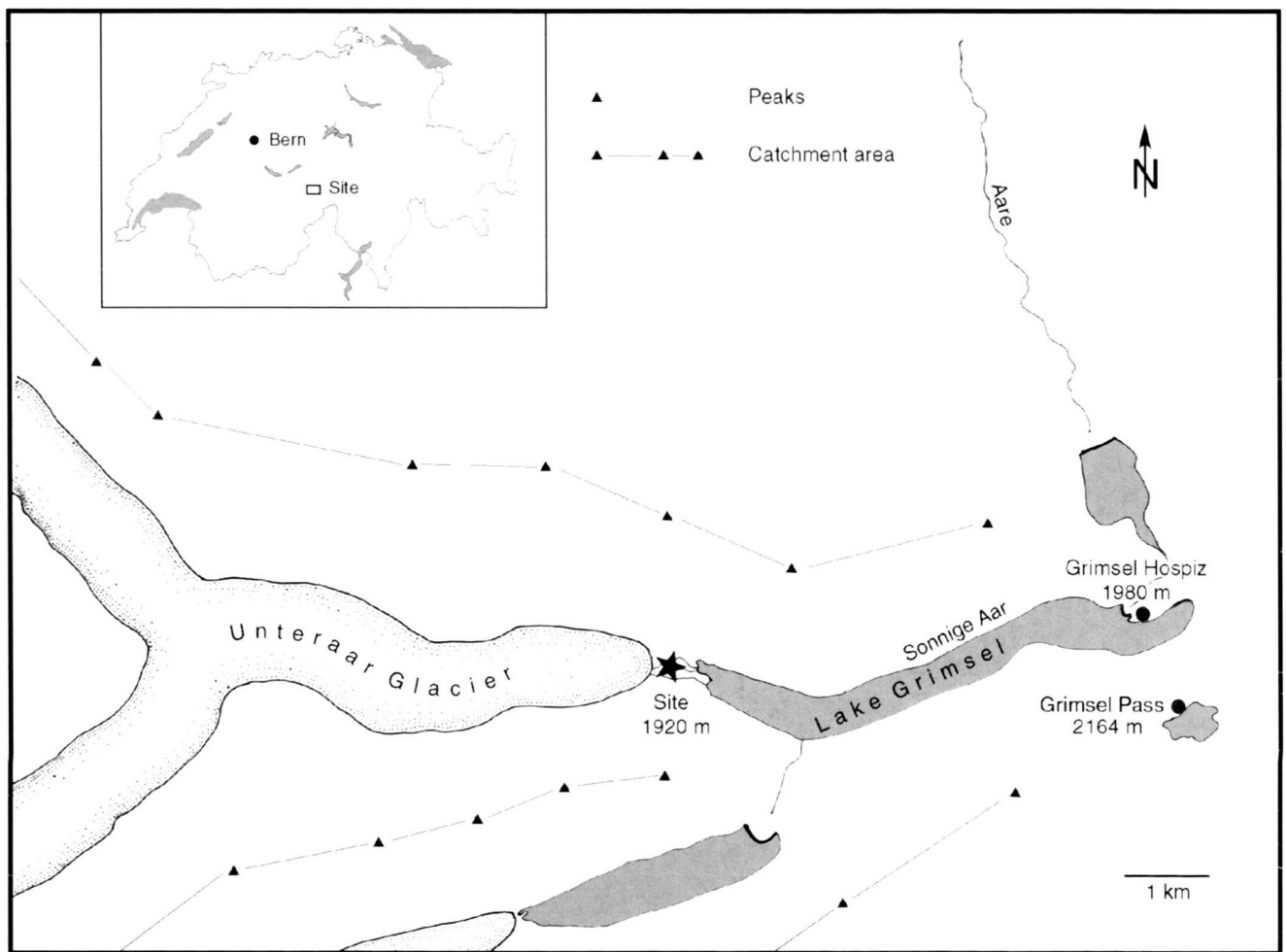


Fig. 1. Map of Switzerland and the Grimsel area with the location of the site

florescence of *Pinus* (not *P. cembra*, pers. comm. M. Winter 1999). We do not consider these facts to be contradictory. It has to be taken into account that the fen peat was located in the Vorfeld of the former glacier where the conditions for tree growth are not favourable due to the unstable geological regime (braided river system). On the vegetation map by Frey (1921), where the situation before inundation is depicted, we find no trees in the Aarboden (Vorfeld / bottom of the valley). He reports that *Pinus cembra*, *Larix decidua*, *Betula alba* prefer to grow on the slopes where they are spread as far as the terminus of the glacier. *Pinus cembra* occurs up to 2100 m a.s.l. on the southerly exposed slope, called "Sonnige Aar" (Fig. 1), and up to an elevation of 2080 m a.s.l. on the northerly exposed slope. A similar situation for the period of 3800–3600 yr BP is conceivable but further upvalley. The fact that the Gletschervorfeld was not forested, indicated by the absence of tree-dependent Coleoptera and the abundance of species living on flowering shrubs and herbs, rules out a tim-

berline much higher than today. This conclusion is supported by other authors who have tried to locate the elevation of timberline in the Swiss Central Alps for this period. Welten (1982), who has made extensive investigations about vegetation history in the Western Swiss Alps, has shown that the era of good alpine forests and high elevation of the timberline lasted until 5000–4000 yr BP. Use by Neolithic man and cattle brought about an end to this period. The event coincides with the mass expansion of *Alnus viridis*. Palaeobotanical data of Tinner et al. (1996) show that Alpe Essertse in the Valais was covered with a forest of *Pinus cembra* and *Larix decidua* up to at least 2343 m a.s.l. from 9500 to 3600 yr BP. After 4700 yr BP the forest became more open and timberline moved down either due to climatic changes or human impact. Wick (in: Wick & Tinner 1997) reports mass expansion of *Alnus viridis* and a continuous downward movement of the timberline at Lago Basso (2250 m a.s.l.) in the Italian Central Alps between 4500 and 3000 yr BP.

Although fluctuation of timberline can indicate climatic changes, estimations of paleotemperatures are difficult to make (Markgraf 1974). A rough approximation is the coincidence of the timberline with the 10°C July isotherm (Eggenberg 1995). Investigations of fossil coleopteran assemblages render a helpful contribution to the question of paleotemperatures (Coope et al. 1998; Ponel et al. 1999).

The period between 4400 and 3600 yr BP is known as the Postglacial Climatic Optimum in the Swiss Alps. Dendroclimatology indicates the longest time span with temperatures above the average between 3760 and 3600 yr BP (Gamper & Suter 1982). For the Eastern Alps, Patzelt suggested mean summer temperatures had been the same as today between 4100 and 3500 yr BP (in: Slupetzky et al. 1998). He postulated (Patzelt 1977) that summer temperatures during the last 9500 years did not fluctuate more than 1.5°C over a longer time span. The study of the fossil beetle assemblage suggests a similar July temperature (9.0°C) at Unteraar between 3800 and 3600 yr BP as today (9.5°C). Calculated mean temperature for the coldest month is -7.7°C compared to the average of the last 35 years at Grimsel Hospiz with -5.3°C in January.

Acknowledgements

In particular I would like to thank Professor Ch. Schlüchter (Bern) who initiated the project and provided the financing. In the Quaternary Entomology Laboratory of Fargo, North Dakota State University, I was introduced to the technique of extracting fossil beetles and collecting living ones in the field. The weeks I spent with Professor A. Ashworth and his team were very stimulating! I am indebted to Professor R. Coope who has always had time to teach me identification during his visits to Switzerland. His valuable comments greatly improved the content of this paper. Many questions were answered by Dr. P. Ponel (Marseille) and Dr. S. Elias (Boulder) and I thank them for their support. I am grateful for the help of several specialists who made or checked the identifications of my beetles: R. Angus, M. Brancucci, M. Döberl, J. Gebert, E. Geiser, C. Huber, B. Klausnitzer, W. Marggi, M. Miler, V. Puthz. Special thanks are due to Dr. A. Zanetti in Verona whose comments on the subfamily of Omaliines improved the accuracy of the faunal list. At the Museum of Natural History in Bern I always felt welcome. I had access to the collection and was given assistance by the members of the Invertebrates Department. With Anne Hormes I had inspiring discussions about the Unteraar peat. It was nice to have someone working on the same site. Many thanks go to Emma Jane Sayer and Dr. W. Shotyk for proof-reading.

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Manuscript received October 28, 1999

Revision accepted May 25, 2000