

Coleoptera from the 2003 excavations of the mammoth skeleton at Niederweningen, Switzerland

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Abstract

A coleopteran assemblage was obtained from a sequence of samples of the peaty matrix of the mammoth skeleton. Altogether 142 beetle taxa were recognised of which 100 could be determined to species, at least 10 of which are now absent from central Europe although many are still living in northern latitudes. This fauna indicates that the organic sediment accumulated in a largely acid swamp with reedy vegetation surrounding mossy pools of shallow water. The only trees at this time were willows, birches and conifers. Palaeoclimatic estimates based on this beetle fauna indicate that mean July temperatures were $\sim 10^{\circ}\text{C}$ and mean January/February temperatures were below -10°C . Thus, the swamp was frozen for much of the year but thawed out during the summer months. One curious aspect of this fauna is the rarity of dung beetles, which would have been expected to be common had the deposit been of exactly the same age as the mammoth. To resolve this anomaly, it is suggested that the mammoth became mired in an already existing swamp during the summer thaw and that the carcass, or at least parts of the body some of which were still articulated, had sunk or was trampled into pre-existing soft mud.

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1. Introduction

Insect remains, especially of Coleoptera, are very abundant in sediments that have remained waterlogged since they were laid down. The fossils from Quaternary deposits can often be identified to the level of species, thus providing an opportunity to make detailed reconstructions of the local palaeoenvironments. Because many species of Coleoptera have repeatedly changed their geographic ranges on an enormous scale in response to Quaternary climatic changes, it has been possible to make quantified estimates of the regional palaeoclimate.

At Niederweningen, the organic matrix in which the mammoth bones were embedded yielded a large number of well-preserved and ecologically varied beetles. These permitted a detailed mosaic picture to be reconstructed of the habitats that were locally available, and also the regional palaeoclimate at the time when the peat accumulated. The rich assemblage of insect remains were recovered from a series of 11 samples of the organic sediments

obtained during the excavation of the mammoth bones at Niederweningen in 2003. The samples' weights are given at the top of [Table 1](#). The insect-bearing deposit was made up of finely divided plant debris with little or no inorganic matter, except for sample 9.9 which included much sand with scattered pebbles. Precise details of the stratigraphic relations of these samples are published elsewhere ([Furrer et al., 2007](#)). Insect fragments were found in all samples, often in great profusion. Occasionally, their flattened remains were visible in the field but, for the most part, the insect remains had to be extracted by disaggregation of the sediment and wet sieving in the laboratory. This methodology is now well known ([Coope, 1986a](#)).

The insect fossils were largely composed of their original chitin (a complex mucopolysaccharide) although the lipids and waxes, which make up part of the original exoskeletons, had been lost. The chitin itself is very resistant to decomposition in anaerobic conditions, particularly where the enclosing sediment has remained waterlogged since its formation. Identification of the insect remains was made by direct comparison of them with well-authenticated modern specimens. The Niederweningen fossil assemblage was composed largely of Coleoptera (beetles). This is because

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Table 1

Data of coleoptera from the Niederweningen mammoth site arranged, as far as possible, in the taxonomic order and according to nomenclature of Lucht (1987)

	97	1	9.1	9.2	9.3	9.4	9.5	9.6	9.7	9.8	9.9	G
Sample numbers FK	97	1	9.1	9.2	9.3	9.4	9.5	9.6	9.7	9.8	9.9	
Sample weights in kg	5.0	1.2	1.8	2.4	3.6	1.0	2.4	0.5	0.8	0.7	1.5	
No. of individuals of each of the species present in the samples												
Coleoptera												
Carabidae												
<i>Carabus arvensis</i> Hbst.	1	1			1							X
<i>Carabus</i> sp.												
<i>Leistus rufescens</i> (F.)							1					
<i>Nebria gyllenhali</i> (Schönh.)	1											
* <i>Pelophila borealis</i> (Payk.)					1							
* <i>Diacheila arctica</i> (Gyll.)	1	2			1							X
* <i>Diacheila polita</i> (Fald.)	1	2			1							X
* <i>Elaphrus lapponicus</i> Gyll.	2	6		2	1	1	1			1		X
<i>Elaphrus riparius</i> (L.)	1											
* <i>Dyschirius nigricornis</i> Motsch.	2				1	1						
<i>Trechus secalis</i> (Payk.)	1											
* <i>Trechus rivularis</i> (Gyll.)	10	1		1	4	15	2					X
<i>Trechus obtusus</i> Er.	2	1				1	2					
<i>Bembidion bipunctatum</i> (L.)	1											
<i>Bembidion obliquum</i> Sturm										1		
<i>Bembidion transparens</i> (Gebbl.)	1				1					1		
<i>Bembidion guttula</i> (F.)					1							
<i>Bembidion</i> spp.	1		1		1							
<i>Patrobus septentrionis</i> Dej.		2		1	3							X
* <i>Patrobus assimilis</i> Chaud.	9	4		2	3	3	4		1	1		X
* <i>Pterostichus brevicornis</i> Kirby		1				1	1					
* <i>Pterostichus blandulus</i> Mill.		3		1								
<i>Pterostichus diligens</i> (Sturm)	15	6		1	5	11	8	1	1	1		X
<i>Pterostichus nigrita</i> (Payk.)	2	4				2	1			1		X
* <i>Pterostichus kokeili</i> Mill.				1	1							
<i>Calathus melanocephalus</i> (L.)					1							
<i>Agonum impressum</i> (Panz.)		2										X
<i>Agonum ericeti</i> (Panz.)	1					1						
<i>Agonum fuliginosum</i> (Panz.)	1				3	1						
<i>Amara quenseli</i> (Schönh.)					1							X
* <i>Amara torrida</i> (Panz.)				1	1							
* <i>Amara alpina</i> (Payk.)		1		2								
<i>Amara</i> sp.							1					
* <i>Chlaenius costulatus</i> Motsch.	1	3			1							X
<i>Dromius agilis</i> (F.)							1					
Dytiscidae												
<i>Hydroporus melanarius</i> Sturm	24	7			1	8	3	2	2	2		X
* <i>Agabus serricornis</i> (Payk.)										1		
<i>Agabus congener</i> (Thunb.) group	2											
<i>Agabus</i> sp.		1										
<i>Ilybius</i> sp.	1	2			1							
<i>Colymbetes paykulli</i> Er		2										
<i>Colymbetes</i> sp.	1				1							
Hydraenidae												
<i>Hydraena cf riparia</i> Kug.	2	2					2			1		
<i>Ochthebius</i> sp.		1										
<i>Helophorus grandis</i> Illiger					1							
<i>Helophorus aquaticus</i> (L.)	2	1			1					1		
<i>Helophorus glacialis</i> Villa	2			1	3	1						
<i>Helophorus</i> sp.	1			1					1	1		
Hydrophilidae												
<i>Coelostoma orbiculare</i> (F.)	14	13		1	1	1	3	3	4	4		X
<i>Cercyon tristis</i> Illiger										1		
<i>Cercyon convexiusculus</i> Steph.	1											
<i>Cercyon analis</i> (Payk.)										1		

Table 1 (continued)

<i>Cercyon sp.</i>	2										
<i>Crenitis punctatostratus</i> (Letzn.)	1							2	1		
<i>Hydrobius fuscipes</i> (L.)	1	1	1		3	1			1		X
<i>Laccobius sp.</i>							1				
<i>Cymbiodyta marginella</i> (F.)	5	8				1	2	1	1	1	
Silphidae											
<i>Thanatophilus dispar</i> (Hbst.)		1									
<i>Phosphuga atrata</i> (L.)	1					1	1				X
Catopidae											
<i>Choleva sp.</i>								1	2		
Colonidae											
<i>Colon spp.</i>	8	1				1	2	1	1	2	
Clambidae											
<i>Clambus sp.</i>							1	1			
Ptiliidae											
<i>Acrotrichis sp.</i>	1										
Staphylinidae											
* <i>Pycnoglypta lurida</i> (Gyll.)	3		1	5	7	1					
<i>Omalium sp.</i>	1										
<i>Olophrum fuscum</i> (Grav.)	3	1		1	7		3		2		X
<i>Olophrum consimile</i> (Gyll.)					1	3			1		X
* <i>Olophrum rotundicolle</i> (Sahlb.)	10	3		7			3	2	3	2	X
<i>Olophrum sp.</i>	3	1		4							X
* <i>Eucnecosum brachypterum</i> (Grav.)	16		1	8	35	5	1	1	3	3	X
<i>Acidota crenata</i> (F.)	6	2			1	3	6		1		X
<i>Acidota quadrata</i> Zett				1							
<i>Hygrogeus aemulus</i> (Rosh.)				1					1		
* <i>Holoboreaphilus nordenskiöldi</i> (Makl.)	1			1	5	1					
<i>Boreaphilus henningianus</i> Sahlb.	2			2					1		
<i>Stenus spp.</i>	91	20	1	19	48	18	17	8	12	27	2
<i>Euaesthetus laeviusculus</i> Mannh.	97	26	1		49	13	24	4	9	16	1
<i>Lathrobium terminatum</i> Grav.	44	14			1	8	13	4	6	7	1
<i>Lathrobium spp.</i>	23	16			3	33	51	12	8	10	X
<i>Cryptobium fracticorne</i> (Payk.)	53	13			1	10	42	11	8	1	
<i>Philonthus punctus</i> (Grav.)	1										X
<i>Philonthus spp.</i>	9	2		1	1	3	4	2	2	2	1
<i>Staphylinus erythropterus</i> L.	1					1	1	1			X
<i>Quedius boops</i> (Grav.) group	11				3	1	6			1	X
<i>Quedius spp.</i>	7				1			1			
Bolitobiinae Gen. et spp. indet	4	1			1	2	3			1	X
<i>Tachyporus sp.</i>	6				2	4	1		1	1	
<i>Tachinus rufipes</i> (Geer)	2	1									
<i>Tachinus corticinus</i> Grav.					1						
<i>Gymnusa brevicollis</i> (Payk.)	2	1			1		2			1	X
Aleocharinae Gen. et spp. indet.	35	10	1	3	5	2	7	9	2	6	1
Pselaphidae											
<i>Bryaxis sp.</i>	1					3	1				
<i>Pselaphaulax dresdensis</i> (Hbst.)					1	4	2	1			
<i>Pselaphus heisei</i> Hbst.	27	1		1	3	10	15	5	2	1	
Elateridae											
<i>Denticollis linearis</i> (L.)	1										
<i>Hypnoidus rivularis</i> (Gyll.)	1			1	1		1				
Helodidae											
Gen et sp. indet	11	3			1		1		2	1	X
Dryopidae											
<i>Elmis aenea</i> (Müll.) or <i>maugettii</i> Latr.	1										
Byrrhidae											
* <i>Simplocaria metallica</i> (Sturm)	2				1						
<i>Cytilus auricomus</i> (Duft.)	5	6		1			4		3	1	

Megaloptera (alder flies) and the larval heads and puparia of Diptera (true flies), but no detailed analysis has been made of these because adequate collections and expertise is not available. Mites were also common and would certainly repay further investigation. The Niederweningen insects are preserved in the Paläontologisches Institut und Museum, Universität Zurich.

2. The fauna

Altogether 142 coleopteran taxa were identified from the samples, of which 100 could be identified to species or species group. At least 20 species are no longer living in Switzerland. Table 1 lists all the species that are arranged, as far as possible, in the taxonomic order and according to the nomenclature of Lucht (1987). Species that do not now live in central Europe have been inserted in their most appropriate place. Species that do not now live in Switzerland are indicated in the table by *. The numbers opposite particular species and in each sample column indicate the minimum number of individuals of that species in the sample. Sample FK 97 and FK 1 were bulk samples taken from the peaty matrix of the mammoth bones. Samples 9.1–9.9 were recovered from a vertical sequence taken through the whole thickness of the organic horizon, which was just over a metre thick at this point: sample 9.1 was at the base and 9.9 at the top of the sequence. Stratigraphical details of these samples are as follows: 9.1 = silt below peat; 9.2 = base of peat; 9.3 = lower part of peat; 9.4 = middle part of peat; 9.5 = middle part of peat below mammoth skeleton; 9.6, 9.7 and 9.8 = upper part of peat correlated with the mammoth skeleton and with FK 97 and FK 1; 9.9 = sandy silt with pebbles above the peat.

3. Local environment interpreted from the coleopteran assemblages

There is no significant difference in the local environments indicated by the coleopteran assemblage from any of the samples. The faunas will, therefore, be viewed as a whole, that is as if they represent a single community. This fauna is largely made up of species, which actually lived in the immediate vicinity, together with some others from further afield that must have been incorporated into the deposit more or less accidentally. The whole beetle assemblage thus provides a mosaic picture, not only of the local environments available nearby but also of more distant ones. Although it is not possible to be precise about the area represented by each assemblage, it is probable that species in these faunas represent habitats that may have been as much as several kilometres around the sampling site.

3.1. Aquatic habitats

The aquatic Coleoptera fall into three main groups: (a) the Dytiscidae and Gyrinidae which are predatory both as

larvae and as adults which are actively swimming species; (b) the Hydrophilidae whose larvae are voracious predators but which in their adult stage feed on rotting vegetation (Hansen, 1987); and (c) the Hydraenidae whose larvae largely feed on algae but whose adults feed on decaying plant debris.

Almost all the aquatic Coleoptera in this assemblage are indicative of stationary water, often in an acid bog. By far the commonest dytiscid in this assemblage is *Hydroporus melanarius*, which is mainly a bog species living in small peaty ponds that are often only seasonal. *Agabus congener* also inhabits small acid ponds. Both *Agabus serricornis* and *Colymbetes paykulli* live in pools with much vegetation. All the hydraenid and hydrophilid species in this assemblage live in small bodies of water that are shallow and may often have been temporary. *Helophorus glacialis* is of particular interest because it is confined to very cold water close to the edges of melting snow patches, where the water is always near freezing point (Hansen, 1987). *Crenitis punctatostriatata* is found in acid bogs where it is associated with *Sphagnum* (Koch, 1989). The semi-aquatic weevil *Bagous* lives on various pond weeds and is capable of swimming underwater (Morris, 1991).

A single specimen of *Elmis aenea/mauetii* is the only representative of the running water community. It is typically found in shallow, fast flowing streams. This habitat must have been extremely uncommon in the immediate surroundings.

3.2. Transitional habitats

This is by far the largest ecological group of beetles in this assemblage. It includes those species that live in the transitional zone between fully aquatic and fully terrestrial habitats, namely in marshes and swamps. Naturally, these environments grade into one another and this group therefore includes species with a greater or less dependency on water.

The Carabidae are chiefly carnivorous or general scavenging ground beetles that often live in damp places. The three most abundant species in this assemblage are *Pterostichus diligens*, *Trechus rivularis* and *Patrobus assimilis*. Taken together, this group indicates that the deposit accumulated in an acid bog probably associated with mossy habitats particularly with *Sphagnum*. The relative abundance of *Elaphrus lapponicus* is interesting because it is characteristic of the mossy surroundings of springs where the water is neutral and on *Hypnum* moss bogs (“Braunmoore”) and is only rarely found on *Sphagnum*. It lives in association with *Diacheila arctica* in similar habitats in northern Sweden (Lindroth, 1985). *D. arctica* itself lives in very marshy places that are overgrown with moss, especially on “quaking ground” formed by species of *Sphagnum* and *Hypnum* (Lindroth, 1992). The habitat of *Chlaenius costulatus* in northern Sweden is described as a mire in thin birch woodland, on soft soil where it occurs in *Sphagnum* hummocks surrounded by pools with *Carex*,

Menyanthes and *Equisetum*, etc. (Lundberg, 1981). It has been caught in the same traps as *E. lapponicus* (Lindroth, 1986), suggesting that the two species have similar habitat preferences. *Bembidion obliquum* is also a swamp species living among clumps of *Carex* and similar plants where the soil is humus rich and very soft. It occurs only singly on *Sphagnum*. *Leistus rufescens* needs wet habitats shaded by tall vegetation. *Pelophila borealis* requires rich plant growth, especially of *Carex*, although it prefers the vegetation to be patchy and the soil to be not covered by mosses. *Pterostichus blandulus* is a species of wet tundras where it can be found under moss and stones (Holdhaus and Lindroth, 1939).

The presence of *Agonum ericeti* is environmentally significant because it is an obligate *Sphagnum*-moor species living in places covered entirely by wet moss (especially *Sphagnum fuscum*). It also lives on drier peaty soils where *Calluna* and similar vegetation is growing. The species requires an acidic soil with pH 3.6–4.6. It is particularly heliophilous and “runs at great speed over the mossy surface during the sunshine” (Lindroth, 1992).

The large number of staphylinid species in this assemblage is made up of predators, which live on small soil arthropods and worms in accumulations of plant detritus in wet places. Their enormous abundance in this fauna indicates that these habitats were locally plentiful. The pselaphid species *Pselaphaulax dresdensis* and *Pselaphus heisei* are also found in decomposing leaf and moss litter including *Sphagnum* (Koch, 1989).

Species of Byrrhidae are among the few animals that feed exclusively on moss, both the larvae and adults grazing on the leaves. In this assemblage, the most abundant byrrhid species is *Cytilus auricomus*, which is, according to Koch (1989), the only central European member of this family particularly associated with *Sphagnum*.

Many of the other phytophagous Coleoptera are restricted in their preferred host plants. Thus, among the Chrysomelidae, *Donacia obscura* feeds largely on the leaves of *Carex rostrata* and also *Scirpus*. *Donacia thalassina* feeds on *Scirpus lacustris* and also on *Glyceria*. *Plateumaris sericea* is found principally on species of *Carex* but also on other waterside plants. Among the Curculionidae (weevils), several species also indicate reedy vegetation. Thus, the northern species *Notaris aethiops*, which is relatively common in this assemblage, and *Notaris bimaculatus* feed on a variety of reeds and sedges (Foster, 2001). *Notaris acridulus* is principally found feeding on the sweet grass *Glyceria*. *Limnobaris pilistriata* is found in swamps and bogs where it also feeds on *Carex*, *Scirpus* and similar plants. Koch (1992) points out that the larvae feed especially on the roots of *S. lacustris*.

Other marsh plants are also indicated by this beetle assemblage. *Phaedon armoraciae* frequently eats the leaves of *Veronica beccabunga* but also *Nasturtium* and *Armoracia*. *Prasocuris phellandrii* feeds largely on aquatic Umbelliferae and the larvae are recorded from *Caltha palustris* (Koch, 1992). *Phyllotreta flexuosa* feeds on

various marsh Cruciferae. The small weevil, *Phytobius*, lives in marshy places where it feeds on the leaves of a variety of plants.

3.3. Drier ground habitats

Not unexpectedly, there are only a few beetle species indicative of dry habitats. Among the carabid ground beetles, *Carabus arvensis* is a xerophilous species on gravel and sand in more or less open country often where there is *Calluna*. *Amara quenseli* requires dry unshaded habitats where the soil is sandy and often mixed with stones and gravel. The sand surface may be loose and unstable. *Pterostichus kokeili* is a tundra and montane species living in relatively dry places. *Amara alpina* is an alpine and tundra species that lives in a wide variety of habitats but is particularly prevalent in the dwarf-shrub heath. Its rarity in this assemblage may be due to the fact that it avoids marshy soils. *Diacheila polita* is usually found on fairly dry peaty soil but also lives at the margins of *Carex* pools on moist soft ground (Lindroth, 1961). The larvae of the small weevil *Orobites cyaneus* develop in the fruit capsules of various species of *Viola*. The high numbers of the phytophage genus *Chaetocnema* indicate the abundance of grass or low herbs although, in the absence of specific identification, it is not possible to be more precise as to which plants were involved.

3.4. Evidence for the presence of trees

Several species in this assemblage are either directly or indirectly dependent on the presence of trees. The beetles indicate that both deciduous and coniferous trees must have been present nearby. *Scolytus ratzeburgi* is a bark beetle that only attacks tree birches, chiefly but not exclusively *Betula alba*, excavating characteristic subcortical galleries in which the larvae develop. It does not utilise dwarf birches. *Melasoma collaris* and *Phytodecta viminalis* feed on the leaves of various species of *Salix*. The minute weevils related to *Rhynchaenus foliorum* mine the leaves of various species of *Salix* and some species of this group attack dwarf willows such as *Salix reticulata*. Most weevils of the *Rhynchites* group are adapted to breeding on deciduous trees. Three species of beetle indicate the presence of coniferous trees. The larvae of *Hylobius abietis* develop under the bark, particularly of *Picea* or, more rarely, of *Pinus*. The weevil *Pissodes* attacks species of both *Pinus* and *Picea*, the larvae developing under the bark. *Hylurgops palliatus* attacks the trunk and larger branches chiefly of *Picea* but also of *Pinus* and *Larix*. The carabid species *Dromius agilis* indirectly indicates the presence of trees, since it is a predator feeding on aphids and other small arthropods in the tops of the trees during the summer months but in winter is found under bark and moss on larger living trees, both deciduous and conifer. The larvae of *Denticollis linearis* develop in rotting wood of deciduous trees in damp situations. Some of the ant jaws from this

assemblage resemble those of the “carpenter ant” *Camponotus*, which makes its nest in rotting tree stumps. The fact that all the above species were rare in this fauna suggests that trees were rather sparse. Furthermore, the relatively large number of carabid species suggesting open or, at most, lightly wooded country also supports this interpretation.

3.5. *Various specialist habitats*

A number of beetle species have habitat preferences that do not easily fit into the above groupings. All the coccinellids (familiar ladybirds) in this assemblage feed principally on aphids with the exception of *Scymnus redtenbacheri* that feeds on coccid scale insects (Majerus, 1994). The larvae of species of *Phalacrus* feed on the spores of smut fungus infecting the inflorescences of grasses and sedges. The adults are found in flowers. *Phosphuga atrata* is a specialist predator on snails. Since no snail shells were found in the sediment, it is probable that any that were originally present must have been subsequently dissolved by the acid water.

3.6. *The curious rarity in this assemblage of beetles associated with dung or carcasses*

Species of *Aphodius* are significant in the interpretation of the large mammal bones in this deposit. These beetles are mostly found in dung upon which they actually feed. It is, therefore, strange that there were so few individuals found in this fossil assemblage. Furthermore, there were none of the other members of the dung community present in this fauna. These observations strongly suggest that there was no dung immediately available in the neighbourhood at this time. Similarly, this fossil assemblage has none of the suite of species that live in carcasses. It is difficult to reconcile this evidence with the contemporary presence of a large mammal either living or dead. In fact, the clear implication of the beetle data is that the large vertebrates whose bones were found in the sediment were not exactly contemporaneous with its deposition. This is an important taphonomic conclusion in that it has consequences for our interpretation and understanding of the relationship of the mammoth skeleton to the deposit in which it was embedded.

It must be emphasised here that, in spite of the taphonomic problems just discussed, the local environments outlined above may provide a real picture of the habitats available to the mammoths and the other mega-vertebrates at this time. The only question at issue is the precise relationship between the skeleton and its matrix. It seems likely that the mammoths became mired in an already existing swamp and that the bones had sunk into the present position in the unconsolidated mud. This scenario becomes more likely when the climatic conditions are taken into consideration. The ground that was frozen solid in the winter would have become a dangerous quagmire as it thawed during the brief summer months.

4. Climatic interpretation of the coleopteran assemblage

One of the most important factors governing the distribution of coleopteran species is the availability of acceptable temperatures. This dependency on suitable thermal climates is reflected in the species' geographical distributions. A considerable number of species of Coleoptera found in the Niederweningen deposits can only be found living today in places that are far away from central Europe. Brief outlines of the ranges of some of the more interesting species will be given here. They will be considered in the same order in which they appear in Table 1.

Pelophila borealis: a circumpolar species whose European range is boreo-British, extending to high latitudes on North America.

Diacheila arctica: a circumpolar species from the extreme north of Fennoscandia eastwards on the Kanin Peninsula, the Pechora region and across Siberia to Kamchatka and northernmost North America. A subspecies is found on the mountains of central Asia.

Diacheila polita: a circumpolar species. In Europe only known from the extreme east of the Kola Peninsula, the Kanin Peninsula, Kolguyev Island and the Pechora region. It ranges across northern Siberia to Alaska and north-west Canada.

Elaphrus lapponicus: a circumpolar species, which, in Europe, has a boreo-British distribution. It is known from eastern Siberia and is widespread in northern Canada and Alaska.

Pterostichus brevicornis: a circumpolar species at high latitudes from the northern and eastern coast of the Kola Peninsula, on the Kanin Peninsula, the Pechora region across northern Siberia to Alaska, and northern Canada with an isolated population on the mountains of the north-east United States. This species also occurs in northern Mongolia.

Pterostichus blandulus: a Eurasian species with a boreo-montane distribution in Europe. In central Europe, it is found in the alpine zones of the High and Low Tatra Mountains. In northern Europe, it occurs on the Kanin Peninsula, Waigatsch Island and Novaya Zemlya and from there eastwards across northern Siberia.

Pterostichus kokeili: a Eurasian species with a boreo-montane distribution in Europe. In northern Russia, it occurs on the Kanin Peninsula and in the Pechora region. In central Europe, it is found at high altitudes in the Eastern Alps, the Eastern Carpathians and the Transylvanian Alps.

Amara torrida: a circumpolar species which in Europe is confined to northern areas of Fennoscandia to the Kola Peninsula, the Kanin Peninsula, the Pechora region and across Siberia to northern North America. It ranges southward along the rocky Mountains as far as Colorado.

Amara alpina: a circumpolar species at all high latitudes and high altitudes further south. In Europe, it is

boreo-British being found in Northern Fennoscandia and at high altitudes further south and only on the highest mountains of the Highlands of Scotland. Its range extends from Europe across Siberia. In North America, its range extends further north than any other carabid species and also at high altitudes in the Rocky Mountains.

Agabus serricornis: a northern Eurasian species widespread in Norway and Finland, but absent from central and southern Sweden, from where it ranges as far as eastern Siberia.

Holoboreaphilus nordenskiöldi: a circumpolar species of high latitudes. In Europe, it is found only in Novaya Zemlya. In central Asia, it is only found in scattered localities in northern Siberia where it is probably under-recorded. It is widespread in northern Alaska.

In addition to these exclusively northern and continental species, there are other northern species present in the Niederweningen assemblage that are also to be found today living at high altitudes in central Europe. Notable among such species are *Patrobis septentrionis*, *Helophorus glacialis*, *Boreaphilus henningianus*, *Eucnecosum brachyp-terum*, *Simplocaria metallica* and *Notaris aethiops*. A few other species such as *Crenitis punctatostrigatus* and *Hygrogeus aemulus* are absent from northern Europe but live today in the mountains of central Europe.

In contrast to these “cold-adapted” species, there are a few others in this assemblage whose present day geographical distributions in Europe barely reach northern Fennoscandia or north-eastern Russia but, nevertheless, their range extends into Siberia. Such species include *Trechus secalis*, *Bembidion guttula* and *Cymbiodyta margin-ella*. The distribution of *Chlaenius costulatus* is curious. It is not found today anywhere in central Europe. It occurs at the northern end of the Gulf of Bothnia and has been recorded from Finnish Lapland. A single individual has been found as far west as Hamburg. The species is widespread in Latvia and Lithuania from where it extends eastwards across Russia to Eastern Siberia.

There can be little doubt that these species viewed as a whole indicate a cold and continental climatic regime. Perhaps the best present day analogue for this climate is that near the northern fringes of the boreal forest in Siberia. In an effort to quantify climatic conditions, the present day distributions of species were plotted on climate space rather than on geographic space. The coordinates of the climate space were defined in terms of the mean monthly temperatures obtained from nearby meteorological stations. In this way, an often ragged geographical distribution of a species would condense into a compact climatic envelope (Coope, 1986b). These envelopes for each species can be easily stored in a database. Palaeoclimatic reconstructions can then be obtained by overlapping the climatic envelopes of the species that occur in a fossil assemblage and reading off the coordinates of the area of maximum overlap (usually 100%). This means of estimat-

ing past thermal climatic conditions has been termed the mutual climatic range (MCR) method and has been described previously (Atkinson et al., 1980). In order to obtain figures that were independent of those obtained from plant evidence, only predatory or scavenging species of beetle were used in these estimates. Although all animals are ultimately dependent on plants for food, these species are not attached to any particular plant and their complex food webs often go back to fungi and algae. It must be emphasised again that these MCR reconstructions of the palaeoclimate are independent of those based on the macrophyte data.

MCR estimates of the palaeotemperature were made using species of Carabidae, Dytiscidae, Hydraenidae, Hydrophilidae and Staphylinidae. Altogether, reliable climatic envelopes for 40 of the species in this assemblage were available on our database. MCR estimates gave the following figures; where T_{\max} is the mean temperature of the warmest month (July) and T_{\min} is the mean temperature of the coldest months (January and February). MCR calculations based on the lowest four samples (i.e. 9.1, 9.2, 9.3 and 9.4) gave the following figures:

T_{\max} , somewhere between 8 °C and 11 °C,

T_{\min} , somewhere between –20 °C and –9 °C.

MCR calculations based on the upper four samples (i.e. 9.6, 9.7, 9.8 and 9.9) gave the following figures:

T_{\max} , somewhere between 12 °C and 13 °C,

T_{\min} , somewhere between –12 °C and –5 °C.

For comparison, the present day air temperatures at Zurich Airport are as follows:

T_{\max} , 18 °C and T_{\min} , –1 °C.

These figures indicate that the mean monthly temperatures probably lay between these limits and not that the temperatures ranged between them. Given a simple sinusoidal curve for the variation in mean monthly temperatures, it is possible to estimate the variation in mean monthly temperatures throughout the year and to arrive at a mean annual temperature. Likewise, it is possible to estimate the number of day degrees above a critical level, available to the plant and animal community. These figures are in accord with the subjective estimation of the thermal climate as being near the northern limit of the boreal forest (Taiga) in Siberia. The MCR climatic estimates suggest that the temperatures at the start of peat accumulation were slightly higher than those at the top. However, both sets of figures clearly show that the surface of the swamp would have been frozen solid during much of the year but would have thawed during the brief summer making precarious footings for any large mammal that crossed it.

The presence of aquatic and marsh beetle species does not necessarily imply that there were high levels of precipitation at this time since, given the above figures

for the temperatures, amounts of evaporation and transpiration would have been relatively low, thus maintaining high values of surface humidity even if the precipitation levels had been low.

5. Comparison of the Niederweningen beetle fauna with other Swiss Full Glacial faunas

The only other Swiss coleopteran assemblages that date from the early or middle Würmian (Weichselian) come from the well-known lignite beds at Gossau, near Zurich. (Jost-Stauffer et al., 2001, 2005). Taken together, the beetle assemblages from both the Upper and Lower lignites from this site bear a remarkable similarity to those from Niederweningen, especially in the occurrence of exotic northern species such as *Diacheila arctica*, *Diacheila polita*, *Elaphrus lapponicus*, *Trechus rivularis* and *Chlaenius costulatus*. The faunas from both Niederweningen and Gossau also included *Agonum impressum* (Panz.), a species that is very rare in Switzerland today (Marggi, 1992). This is predominantly an eastern species with a range extending across Siberia as far as Kamchatka. In Europe, it reaches only as far west as The Netherlands and north-east France. All the coleopteran species in this assemblage that are also found at Gossau are indicated by X on the right-hand side of Table 1 in column G. The Gossau fauna also included exotic species not found at Niederweningen. These include the high northern species *Pterostichus middendorfi* (Sahlb.) whose nearest present day locality is on the Kola Peninsula and the Asiatic species *Carabus meander* Fisch whose closest present day occurrence is at Tjumen, West Siberia ~3000 km to the east of Switzerland (Jost-Stauffer et al., 2001).

These Swiss Full Glacial coleopteran assemblages bear many similarities to other faunas of the same general age, in particular those from the British Isles (e.g. Coope, 1968) where many of the exotic species mentioned here have also been found, suggesting that there might have been a broadly similar insect fauna throughout much of northern and central Europe at this time and that this fauna was very different in its species composition from that found anywhere in Europe at the present day.

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